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STATUS OF LAKE WHITEFISH (*COREGONUS CLUPEAFORMIS*) IN LAKE
CHAMPLAIN, 2006-2010

A Thesis Presented

by

Seth J. Herbst

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements
for the degree of Master of Science
Specializing in Natural Resources

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ABSTRACT

Lake whitefish (*Coregonus clupeaformis*), in the family Salmonidae, is a coldwater species that is widely distributed in North America. Throughout their range, whitefish support one of the most economically valuable freshwater fisheries and were also commercially fished in Lake Champlain. My goals were to quantify seasonal diet, determine temporal and spatial changes in larval abundance, evaluate biological parameters (size and age structure, sex composition, growth, condition, energy density, and fecundity), and determine if the introduction of zebra mussels (*Dreissena polymorpha*) to Lake Champlain in 1993 had similar effects on the whitefish population as seen in many of the Great Lakes. Whitefish were collected year-round using gillnets and bottom trawls. Diet was quantified seasonally. Temporal and spatial changes in larval abundance were determined by ichthyoplankton net catches. A comparison of scales, fin rays, and otoliths indicated that otoliths provided the lowest bias and highest precision. Age estimation using otoliths generated a wider range of ages and greater number of age classes when compared with scales and fin rays and therefore age and growth were determined using otolith age estimates. Growth parameters of the entire main lake population were estimated using the von Bertalanffy growth model ($K = 0.20$; $L_{\infty} = 598$ mm), mean condition using Fulton's K condition factor ($K = 1.05$) and by determining energy density, and fecundity using the gonadosomatic index ($GSI = 13.9$). Larval whitefish were abundant throughout much of the main lake, but absent in Missisquoi Bay and rare in Larabee's Point, the historic commercially fished locations. Diet varied seasonally; whitefish fed primarily on large numbers of fish eggs in the spring and transitioned to foraging on mysids in the summer and gastropods in the fall and winter. Surprisingly, zebra mussels made up less than 1% of the diet and appeared in less than 10% of the stomachs analyzed, despite being abundant in the benthos. Biological parameters (size and age structure, sex composition, growth, condition, energy density, and fecundity) of whitefish in Lake Champlain were typical of an unexploited population, with multiple length and age classes represented. Condition was high and representative of a diet with high energy content. Whitefish in Lake Champlain had similar high energy density to those in Lake Erie, where declines in whitefish condition were not associated with dreissenid invasions, and had greater mean energy density than whitefish in lakes Michigan, Huron, and Ontario. I concluded that the current whitefish population in the main lake of Lake Champlain is typical of an unexploited population. However, whitefish apparently no longer use Missisquoi Bay and Larabee's Point for spawning, most likely because of human alteration of habitat conditions. The high condition factor and energy density of whitefish in Lake Champlain, in contrast to the Great Lakes, is probably a result of their ability to attain sufficient energy sources from an intact native forage base.

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LITERATURE REVIEW

Introduction

Lake whitefish (*Coregonus clupeaformis*), a member of the family Salmonidae, is a cold-water species that is widely distributed in North America. The range of lake whitefish extends from the Atlantic coastal watersheds westward across Canada and the northern United States to British Columbia and Alaska (Scott and Crossman, 1973). Lake whitefish (hereafter, whitefish) throughout their range are one of the most economically valuable freshwater fishes in North America (Mills et al., 2004). The Great Lakes support the largest, most valuable whitefish fisheries. In 2008, 9.55-million pounds of whitefish, valued at US\$8.1-million dollars, were harvested from the US waters of the Great Lakes (NMFS, 2008). In 2006, Canadian fisheries in the Great Lakes harvested 7.1-million pounds valued at CAN\$9.1-million (Fisheries and Oceans Canada, 2006).

Historically, Lake Champlain supported a thriving fall commercial fishery for whitefish. Whitefish were commercially harvested by seining from 1893 to 1904 in Vermont waters of Lake Champlain; however, following public concern about potential over-harvesting of whitefish, the Vermont legislature outlawed netting following the 1904 season. In 1910, the Vermont legislature once again authorized commercial license sales to fish with nets in Lake Champlain. Following this re-authorization, Vermont sold as many as 64 commercial licenses and the harvest yielded as much as 70,000 pounds of whitefish annually. The commercial fishery continued in Vermont waters until the fall of 1912 when the last record of commercial seine fishing for whitefish was documented (Halnon, 1954, 1963). Despite the closure in U.S. waters, the commercial fishery has

continued in the Canadian waters of Lake Champlain (Missisquoi Bay) with limited success. License sales and whitefish harvest have declined in the Canadian fishery since the early 1900s (Halnon, 1954, 1963). Limited fishing success led fishermen to voluntarily cease fishing and the fishery has been dormant in Canadian waters since 2004 (Miller personal comm., 2006). Following closure of the commercial fishery in U.S. waters of Lake Champlain, whitefish numbers were low during biological surveys in 1930, 1953, and 1954, and the 1970s (Greeley, 1930; Halnon, 1954, 1963; Anderson, 1978a). Van Oosten and Deason (1939) conducted the only published study of age and growth of whitefish in Lake Champlain. The population status of whitefish is currently unknown in Lake Champlain.

Threats to Population Stability

Historically, whitefish abundance in the Great Lakes has fluctuated which is likely a result of overexploitation, anthropogenic changes, predation and competition by exotic species, and environmental conditions affecting recruitment (Cook et al., 2005; Hoyle, 2005; Nalepa et al., 2005). Whitefish have been exploited throughout their range because of their commercial value making them susceptible to overexploitation, which over time has the ability to negatively impact abundance by removing large, mature fish from a population (Van Den Avyle and Hayward, 1999). Declines of whitefish populations within the Great Lakes have also been attributed to the negative impacts of the introductions of exotic species such as rainbow smelt (*Osmerus mordax*), alewife (*Alosa pseudoharengus*), and sea lamprey (*Petromyzon marinus*) (Ebener, 1997). Introduced rainbow smelt and alewife have negatively impacted whitefish populations,

primarily through larval predation. In a Canadian inland lake, predation on larval whitefish by rainbow smelt was intense due to the coincidence of peak hatching activity of whitefish with peak rainbow smelt spawning activity (Loftus and Hulsman, 1986). Sea lamprey are fish parasites that feed on the body fluids of their host, weakening and making the host more vulnerable to disease and subsequent mortality. For perspective, in the northern portion of Lake Huron, an estimated 75% of sea lamprey attacks on whitefish from mid-June to mid-November were fatal (Spangler et al., 1980). Whitefish stocks throughout many of the Great Lakes have also been impacted by the exotic zebra and quagga mussels (*Dreissena polymorpha* and *D. bugensis*). Dreissenids likely caused a population collapse of the major prey of whitefish, the burrowing amphipod *Diporeia*, causing diet shifts towards less energetically valuable prey and resulting in decreased growth and condition of whitefish in the Great Lakes (except Lake Superior) (Mohr and Nalepa, 2005).

Anthropogenic changes may also have contributed to declines in whitefish abundance. Historically, land use has changed aquatic ecosystems through inputs of pollutants, phosphorus, and increased sediment. Decreases in dissolved oxygen have been attributed to increased levels of phosphorus, which elevate primary productivity. Increases in productivity, because of nutrient loading and siltation, cause eutrophication, which can negatively impact species such as whitefish that require cold, well-oxygenated waters and silt-free substrates for egg survival (Taylor et al., 1987). Sediments cover hard, stony substrate and can cover and suffocate eggs, causing high egg mortality and decreased recruitment (Evans et al., 1996). In Lake Erie, reduced catches of whitefish were reported following years of low recruitment that were associated with years of

increased siltation on spawning areas (Trautman, 1981; Cook et al., 2005). Although major fishery declines in Lake Champlain have not been attributed to anthropogenic changes in land use, the potential that land use has affected the lakes fisheries is present, especially in Missisquoi Bay and south lake locations. Phosphorus and nitrogen concentrations in the south lake are, on average, higher than any other location in Lake Champlain (Lake Champlain Basin Program, 2008). Habitat alterations in south lake locations near Ticonderoga, NY was a result of discharges of logging waste, sewage, and pulp and paper waste effluent in the late 1800s. These discharges created a high organic matter “sludge” bed in the area (Myer and Gruendling, 1979). High concentrations of phosphorus and nitrogen, along with low cation concentration and alkalinity, also suggest significant loading from man-made sources in Missisquoi Bay (Myer and Gruendling, 1979). These changes, along with the multiple factors previously mentioned, are detrimental to whitefish recruitment, thus increasing the vulnerability of whitefish populations.

Diet

Information about the quality and quantity of food in the diet of fishes is important for understanding factors that influence productivity, growth, and condition (Bowen, 1996). Whitefish are benthivores, feeding primarily on bottom-living invertebrates and occasionally feeding on small fish (Scott and Crossman, 1973). Prey items that are consistently in whitefish diets include amphipods, molluscs, dreissenid mussels, insects, zooplankton, fish, and fish eggs. Whitefish can be non-selective feeders,

showing variations in diet among different lakes, seasons, and depths that are often consistent with prey availability (Hart, 1931; Pothoven, 2005; Pothoven and Nalepa, 2006; Pothoven and Madenjian, 2008; Seider and Schram, in review). An example of a non-selective feeding pattern is the increased consumption of dreissenid mussels by whitefish following increased abundance of the non-native mussels into many of the Great Lakes (Ihssen et al., 1981; Pothoven and Nalepa, 2006; Pothoven and Madenjian, 2008).

Amphipods, particularly *Diporeia* spp. and *Mysis diluviana*, are major prey items of whitefish. Qadri (1961) in Lac la Ronge, Saskatchewan, reported small quantities of amphipods in stomachs of almost every main lake sample, and in Hunter Bay amphipods constituted 44 to 90% by volume of stomach contents. Similarly, Larkin (1948) concluded that 60% of whitefish food in Great Slave Lake was *Diporeia*. Amphipods are also important prey items in many of the Great Lakes (Lake Erie: Cook et al., 2005; Lake Superior: Seider and Schram, in review; Lake Ontario: Owens and Dittman, 2003; Lumb et al., 2007). Historically, whitefish relied largely on the abundant benthic amphipod *Diporeia* as a high-energy food source in the Great Lakes (Ihssen et al., 1981). The proportion of *Diporeia* in the diet in various areas of Lake Michigan was directly related to *Diporeia* abundance in those areas (Pothoven, 2005). However, following dreissenid mussel invasion in the late 1980s through the 1990s, abundance of *Diporeia* in the benthos and in whitefish diets declined (Mohr and Nalepa, 2005).

Molluscs, particularly gastropods, sphaeriids, and dreissenid mussels are common dietary items of the whitefish. Gastropods and sphaeriids have been reported as a prey item in all the Great Lakes and the majority of other inland lakes studied (Lake Michigan:

Pothoven et al., 2006; Lake Ontario: Hart, 1931; Hoyle et al., 1999; Owens et al., 2003; Lake Erie: Cook et al., 2005; Lumb et al., 2007; Lake Huron: Pothoven and Nalepa, 2006; Rennie et al., 2009; Lake Superior: Seider and Schram, in review; misc. lakes: Van Oosten and Deason, 1939; Larkin, 1948; Qadri, 1961; Ihssen et al., 1981). Sphaeriids, for example, were the the most abundant prey item (% wet mass) in spring, summer, and fall in Lake Erie (Lumb et al., 2007). Often the abundance of molluscs in the benthos makes them readily accessible to foraging whitefish. Following the proliferation of dreissenids in the benthos, they have become a major component of whitefish diet in the Great Lakes (Lake Erie: Cook et al., 2005; Lumb et al., 2007; Lake Michigan: Pothoven et al., 2001; Pothoven and Madenjian, 2008; Lake Huron: Pothoven and Nalepa, 2006; Pothoven et al., 2006; Pothoven and Madenjian, 2008; Lake Ontario: Hoyle et al., 1999; Owens and Dittman, 2003; Lumb et al., 2007; Rennie et al., 2009). For instance, large whitefish in Lake Huron ate primarily molluscs, and of those molluscs 96% were quagga mussels (Pothoven et al., 2006). Similarly, quagga mussels were eaten by 50% of large whitefish (> 350 mm) and accounted for 78% of the diet by weight in those fish from Lake Huron (Pothoven and Nalepa, 2006).

Insects and fish eggs are often seasonally available in the benthic habitat occupied by whitefish, thus making them potential prey items. Because many diet studies of whitefish are conducted over a short period, often in summer, when prey items such as fish eggs and various aquatic insect larvae are not present; these items may be missed in the diet. Multi-season diet studies, in contrast, often report the presence of fish eggs and insects. For example, Seider and Schram (in review) reported that fish eggs occurred in 66% of stomachs analyzed during the winter in Lake Superior. Fish eggs were also a

major component of whitefish diet following ice-out in Lake Champlain (unpublished data, this study). Seasonally available prey items such as caddis-fly larvae, dipteran larvae, and mayfly nymphs were in stomachs of whitefish (Qadri, 1961; Hoyle et al., 1999). Another major prey item of whitefish is chironomid larvae (Hart, 1931; Larkin, 1948; Cook et al., 2005; Pothoven and Nalepa, 2006). For example, chironomids made up 39-64% by volume of the prey items of whitefish in Lac la Ronge, Saskatchewan (Qadri, 1961).

Whitefish can be opportunistic feeders, occasionally feeding on small fish. Fish species in whitefish diets include rainbow smelt, darters, sculpin, and other small species (Scott and Crossman, 1973; Seider and Schram, in review; unpublished data, this study). Seider and Schram (in review) found that fish, primarily smelt, accounted for 19% of the diet by composition during the winter season in Lake Superior.

Ontogenetic dietary changes are typical in whitefish. Larval and juvenile whitefish feed primarily on zooplankton (Hoagman, 1973). Hart (1931) found that for the first five years whitefish fed heavily on plankton in Lake Ontario. Similarly, Cook et al. (2005) reported that zooplankton were common components in the diet of young-of-year whitefish in Lake Erie. Although zooplankton is primarily preyed upon by younger, smaller whitefish, zooplankton has been reported in stomachs of whitefish of all sizes (Ihssen et al., 1981; Tohtz, 1993; Pothoven et al., 2006).

Information on diet and prey items of fishes is valuable because it relates to the amount of energy a fish acquires for the energetic costs of growth, reproduction, and maintenance (Wootton, 1990). Foraging models based on optimal foraging theory assume that individuals maximize their net rate of food consumption. Net food consumption is

measured as the gross energy content of the food minus the energetic cost of acquiring it (Wootton, 1990). Prey items vary in abundance and energetic value in natural systems, directly influencing the energy intake and growth of fish. Energy used for locating, capturing, handling, and processing food is diverted from growth, and therefore quality of food items selected may explain growth variations among populations (Ihssen et al., 1981). Data on the quality and quantity of diet items are valuable for understanding trends in biological attributes of predators (growth, condition, and age at maturity).

The benthic community shifts caused by dreissenid mussel introductions, previously mentioned, have resulted in decreases in the energy density of whitefish, as shown using bioenergetics modeling (Madenjian et al., 2006; Pothoven et al., 2006; Lumb et al., 2007). The primary concern regarding decreases in whitefish energetic value is the implication for growth. A surrogate for estimating growth potential of whitefish is to estimate their energy density, which is controlled by two factors, (1) energy content of a fish's diet and (2) feeding rate (Madenjian et al., 2000). For comparison, estimates of energy densities of whitefish primary prey items are 3,625 J/g for *Diporeia* and 3,924 J/g for *Mysis*, relative to 1,703 J/g for dreissenid mussels (Madenjian et al., 2006). There are also processing costs associated with consuming large quantities of shelled prey (Pothoven et al., 2001; Owens and Dittman, 2003). Pothoven and Nalepa (2006) found that energy in whitefish stomachs was lowest for fish that ate shelled prey. Similarly, Pothoven and Madenjian (2008) suggested that to achieve pre-invasion growth rates with the post-invasion diet composition, total consumption would have to increase by 78-122% on average over observed post-invasion consumption in Lake Huron because of the lower energetic intake from preying upon dreissenids.

Age Estimation

Age data from fish populations are valuable for modeling population dynamics to understand trends in growth, age at maturity, and estimates of mortality, all of which aid fisheries managers in making decisions (DeVries and Frie, 1996; Campana, 2001) . The use of inaccurate ages can cause severe errors in fish population management (Beamish and McFarlane, 1983; Yule et al., 2008). Given the importance of accurate estimates of age, in recent years fisheries scientists have focused on the importance of validating and comparing the various aging structures (Mills and Beamish, 1980; Beamish and McFarlane, 1983; Muir et al., 2008a; Bruch et al., 2009; Davis-Foust et al., 2009).

Fish age is estimated by examining a fish's hard parts or bony structures. The three most commonly used hard parts are scales, otoliths, and fin rays. The theory behind age estimation is based on the appearance of annular checks or annuli. Formation of annuli is thought to be related to differing seasonal growth patterns in fish, resulting from rapid growth in the spring and summer and slow growth in winter (DeVries and Frie, 1996). In general, otoliths and, to a lesser extent, fin rays provide a better representation of the permanent record of fish growth in comparison to scales and therefore give a better estimate of age (Beamish and McFarlane, 1987).

Age has been examined in whitefish beginning in the late 1920s, initially using scales. The scale method was described by Van Oosten (1929) and is still used for routine age estimation for whitefish by some state agencies. The justification of the scale method of age estimation was published by Van Oosten (1923), using scales from whitefish held in the New York Aquarium (an artificial environment) for a known period of time; in this

study he determined that annuli were formed annually. However, tagged whitefish in Little Moose Lake, New York, failed to form a scale annulus between marking and recapture (Neth, 1955). Such discrepancies led fisheries professionals to begin to test for precision and accuracy of aging structures, using techniques later described by Campana et al. (1995). Comparisons have been made between scales, fin rays, and otoliths for many whitefish populations (unexploited and exploited) to determine which aging structure is most precise and easy to use. In whitefish populations, scales commonly underage fish in comparison to estimates from fin ray and/or otoliths (Barnes and Power, 1984; Mills et al., 2005; Hosack, 2007; Muir et al., 2008a; Seider and Schram, in review). For example, Power (1978) reported that otolith ages could be more than double those based on scales for unexploited whitefish from lakes in northern Quebec. Comparisons of fin ray ages with scales gave similar results; for instance, Mills and Beamish (1980) examined 15 populations of lake whitefish and found that fin-ray ages were frequently greater than scale ages for southern as well as northern unexploited populations. Mills and Chalanchuk (2004) and Mills et al.(2004) demonstrated that otoliths and fin rays from lake whitefish tagged and subsequently recaptured provided more accurate age estimates than did scales for slow growing, unexploited stocks. Comparisons of fin ray to otolith age estimates are less documented in the whitefish literature, with limited results reporting little to no difference between the age estimates from these two structures (Mills and Chalanchuk, 2004; Muir et al., 2008b).

Comparisons among aging structures are valuable because age determined from different structures taken from an individual fish often do not agree, due to difficulty in identifying the first annulus, clustering of annuli on the edge of the structure, or poor

preparation of the structure for aging (Campana, 2001; Mills and Chalanchuk, 2004). Clustering of annuli on the edge of a structure is common among older individuals with slow growth rates. Given that growth is variable among populations, the most precise and accurate aging structures may vary among bodies of water. Muir et al. (2008b) deemed that use of fin rays for age estimation was the most practical based on the precision of the age estimates and overall lower cost of preparation; however, this evaluation can be quite subjective in regards to cost from agency to agency. Therefore, it is useful to examine precision, cost, and ease of preparation and structure reading for any new population under study.

Growth and Condition

Growth-

Fish growth data are widely used by managers to evaluate health, production, and habitat quality of fish populations. Increased growth rates result in fish quickly reaching desirable sizes for anglers. As poikilotherms, growth is indeterminate in fish, meaning that individuals have no innate limits to growth and can continue to increase in size throughout life (Van Den Avyle and Hayward, 1999). Growth is defined as the change in body size over time, measured by determining length at a given age (DeVries and Frie, 1996), and is generally estimated using the von Bertalanffy growth model. The von Bertalanffy growth model is based on the theory that the rate of change in length per unit of time will get smaller and approach zero as a fish nears its maximum possible size (Van Den Avyle and Hayward, 1999). Growth patterns in fish are related to the amount of

energy taken in through food consumption that can be retained within the body and not utilized for maintenance and reproduction (Wootton, 1990). Multiple factors affect the amount of energy resources a fish can acquire, which in turn, has direct implications for growth.

Population attributes, such as growth, are influenced by density-dependent processes that regulate population size. Density-dependent factors including food availability, predation, cannibalism, diseases, parasites, and availability of spawning sites, vary with population size. These factors usually operate in a compensatory manner, so that extremes in population size are moderated by their action. For example, with increasing fish population density, food availability per fish declines, leading to slower growth and poorer condition of the surviving fish (Van Den Avyle and Hayward, 1999). Whitefish have shown changes in growth due to density-dependent factors, with slow growth in years of increased abundance (Healey, 1980). Similarly, Wright and Ebener (2005) found lower growth rates when population abundance and biomass were high. Exploitation reduces the population size in a system, thus influencing the density-dependent responses of the exploited population. Whitefish, given their commercial value, have been exploited by commercial fishermen in many parts of their native range. Varying levels of exploitation have lead to fluctuations in whitefish growth; high exploitation led to increased growth and minimal exploitation led to decreases in growth in Canadian lakes (Bell et al., 1977).

Food quality and quantity are pertinent to growth performance when looking at growth from a bioenergetics viewpoint. The bioenergetics equation simply states that growth is an output based on an input, food consumption. Quality of food varies in

energy, nutrient content, and in the size of food particles. Therefore, differing quality of food, measured in energy intake, impacts growth output (Wootton, 1990). Energy input during consumption is offset by the search, capture, handling and processing of food, therefore taking away from growth potential (Ihssen et al., 1981; Wootton, 1990). Optimal growth results from low energetic costs of acquiring and handling prey and through consuming prey items with high energetic value (Wootton, 1990). Prey items that are larger in size tend to be more energetically rich and thus valuable for growth (Pothoven and Nalepa, 2006). For example, mean weight of whitefish adjusted for length declined significantly in 1992-1999 in southern Lake Michigan compared with historic records; the change is thought to be due to diet change from *Diporeia* to less energetically valuable prey items (Pothoven et al., 2001). Similarly, declines in whitefish growth and condition have occurred in the main basin of Lake Huron, especially over the last 10 to 15 years, as a result of diets that contain only 57% of the pre-dreissenid invasion energy (McNickle et al., 2006). Likewise, preliminary data reported by McNickle et al. (2006) suggested that the growth rate of whitefish in South Bay, Lake Huron between their 2nd and 3rd year is 47% lower following the zebra mussel invasion.

Climatic conditions, particularly temperature, can directly and indirectly affect fish growth. Temperature has a direct effect on the rates of food consumption and metabolism in fish, and therefore has implications for growth (Wootton, 1990). Fish species have optimal temperature ranges for consumption and metabolism, such that when optimal environmental conditions are not available, growth is affected. Whitefish require a cold-water refuge during the summer months when water temperatures are high. If such a refuge is unavailable, changes in the rate of food consumption and metabolism

could negatively impact whitefish growth rates. Temperatures below an optimal range decrease feeding activity and slow down metabolic rates, decreasing growth.

Temperatures above a desired temperature range increase metabolic rates to the point that fish cannot acquire enough energy through food consumption (Wootton, 1990).

Although negative impacts have not been documented to date, global climate change could therefore potentially have dramatic effects on whitefish populations, especially on populations in the southern portion of their range. Temperature and ice cover also affect recruitment, which in turn influences population size (Taylor et al., 1987). Because population size influences growth through density-dependent processes, growth is indirectly impacted by temperature.

Variations in growth rates of individual fish of the same species is common, however there is usually a range of sizes corresponding to the age at which that species becomes sexually mature. These species-typical sizes are evidence that a genetic component has a role in determining the pattern of growth (Wootton, 1990). Age at maturity relates to the genetics of a species and also has implications for growth. Following maturation, fish often have lower growth rates because energy intake is now allocated to gamete production in addition body growth and maintenance (Wootton, 1990). In whitefish, age at maturity is variable, with males usually maturing at a younger age than females but having a shorter life expectancy (Scott and Crossman, 1973). Males have been found to mature as early as the end of their second year of life (Van Oosten and Hile, 1949), but more commonly maturity ranges from roughly 3.5 years to 8 years old on average and females from 4.5 years to 8 years old on average (Beauchamp et al., 2004; Hosack, 2007; Lumb et al., 2007). Law (2000) and Conover and Munch (2002)

theorized that intense fishing efforts over a sustained period of time can exert powerful selective forces that can have lasting effects on the genetics of fish populations, resulting in slower individual growth rates. The proposed mechanism for this theory is that faster growing fish are harvested more heavily because they reach the minimum length requirement more quickly than slower growing members of their cohort, thus reducing the probability that the faster growing fish will reproduce before being harvested.

Kratzer et al. (2005) tested this hypothesis on whitefish in areas throughout the Great Lakes and reported no evidence to indicate that the slower growth rates of whitefish were related to changes in the genetics of these populations. Whitefish in Lake Superior exhibited the smallest decline in growth over the time studied, yet had the highest fishing mortality, which was contradictory to the intense fishing hypothesis (Law, 2000; Conover and Munch, 2002).

Condition-

Condition is the measure of the energetic status, well-being or health of a fish population and is an important metric used by fisheries managers for assessing population attributes (Froese, 2006). Condition incorporates the measure of an individual's weight at a given length, and is therefore an indirect measure of growth (Anderson and Neumann, 1996). Multiple length-based condition indices are available based on the premise that fish with greater mass than other individuals of the same species of similar length are considered to be in good condition, with biological reference points differing among the indices (Anderson and Neumann, 1996; Froese, 2006; Rennie and Verdon, 2008). Fulton's K condition, for example, assumes that fish growth is isometric (Froese, 2006). Condition is most dependent on food source and metabolic costs (Ney, 1999). Therefore,

the declines in whitefish growth the Great Lakes following dreissenid invasion also resulted to declines in condition (Pothoven et al., 2001). However, one major difference between condition and growth is the use of condition for understanding seasonal effects.

Condition is the relationship between weight and length in fish. Length at a given age stays relatively constant throughout the year, but fish weight can vary dramatically by season, especially in sexually mature fish (Anderson and Neumann, 1996; Froese, 2006). Bias can be incorporated into condition indices if differences in sex, sexual maturity, and seasonal variation are not examined (Froese, 2006; Rennie and Verdon, 2008). However, seasonal estimates of condition can be useful as an inexpensive, easily measured surrogate to predict reproductive capability. This use of condition estimates is based on the assumption that sexually mature fish that are heavier for a given length are potentially more fecund (Anderson and Neumann, 1996).

Fecundity

Fecundity estimates are valuable for relating the life history strategy of a population and the allocation of limited energy resources towards growth, reproduction, and maintenance (Ware, 1982). Reproductive success in fishes has been linked to life history strategy of individual species, which often relates to how fecund or how many eggs an individual can produce (Wootton, 1990). Therefore, it is important to also gain an understanding of the fecundity of a fish species which can have implications for recruitment. Fecundity, the total number of eggs produced by each female, can be useful in estimates of recruitment. Generally, the higher number of eggs, or amount of energy

incorporated in each egg, the higher probability of large year class strength (Brown and Taylor, 1992).

Whitefish have variable fecundity and energy content within each egg, both annually and between populations (Healey, 1978; Healey and Dietz, 1984; Kratzer et al., 2007). In the Great Lakes, fecundity estimates (number of eggs per pound of fish) have varied from 8,200 in Lake Huron, to 9,900 in Lake Ontario, and 16,100 in Lake Erie; fecundity (total egg count) ranged from 18,433 to 58,567 in two Canadian lakes (Lawler, 1961; Christie, 1963; Cucin and Regier., 1965; Healey and Dietz, 1984). Variations in fecundity can be caused by many factors, one of which is differences in available energy resources. Available energy resources for whitefish populations are often related to density-dependent factors, and can impact the population dynamics. Similar to growth and condition, fecundity is impacted by population density. Kratzer (2007) found that fecundity and whitefish abundance were inversely related at five locations within Lake Michigan. Compensatory responses are common in fish populations that face increased levels of exploitation (Van Den Avyle and Hayward, 1999). Fish populations compensate for exploitation in many ways, one of which is increased fecundity, which can lead to years of high recruitment (Healey, 1978, 1980; Kratzer et al., 2007). Fecundity is also influenced by constraints of female body size and egg size because of limited body cavity space. Egg size was positively correlated with female body size among five whitefish populations in the Great Lakes region, however, the egg size to fecundity relationships showed high variability between those same five whitefish populations (Ihssen et al., 1981). Similarly, fecundity was relative to female whitefish growth, with fish of greater mean length producing higher numbers of eggs in exploited Canadian lakes (Bell et al.,

1977; Healey and Dietz, 1984). Knowledge of whitefish fecundity can aid in the modeling of population dynamics and develop an understanding on the population's life history strategy.

Reproduction and Recruitment

Whitefish spawning occurs in the fall, generally in November and December in the southern portion of the range and earlier in the northern portion of their range. Leading up to spawning, whitefish move from deeper water to littoral areas (Bégout Anras et al., 1999). Upon arriving at suitable spawning habitat, spawning activity occurs at temperatures ranging from 4.5-10.0 °C in shallow waters, often less than 9 m. The first spawning run of fish is frequently dominated by small males (Hart, 1930; Scott and Crossman, 1973). In Lake Erie, spawning generally concludes when water temperatures reach 5.7 °C, the predicted temperature corresponding to fifty percent of spent females (Cook et al., 2005). Whitefish have been found to spawn on various types of substrate; however, preferred spawning substrate consists of hard or stony bottoms with boulders and small cobble (substrate sizes were undefined), with suboptimal substrate consisting of sand and detritus (Scott and Crossman, 1973; Bégout Anras et al., 1999). In northern Lake Michigan, whitefish spawning was concentrated over stony or gravel substrate in water less than 5 m deep, taking place primarily at night, when females release eggs randomly over the spawning grounds (Hart, 1930). Competition for the most suitable spawning sites is possible when population density is high, whitefish concentrated at the best available sites during low population densities in South Bay, Lake Huron, thus

suggesting that substrate quality is likely important to the spawning biology of whitefish (Ihssen et al., 1981).

Following fertilization, eggs incubate on the spawning grounds until they hatch in April or May, dependent upon water temperature (Scott and Crossman, 1973). Laboratory studies have shown that fertilized eggs incubated in aerated lake water at constant controlled water temperatures hatched at temperatures ranging from 0.5 to 10.0 °C. The optimal temperature regime for hatching occurred at a range of 0.5-6.0 °C, with length at hatching and swimming activity being greatest at 0.5 °C (Price, 1939). Lab studies are beneficial for understanding the biology of a species, but environmental conditions are often not as stable as laboratory conditions. Whitefish in natural environments hatch at temperatures in the range reported by Price (1939), but most of the hatching literature on whitefish simply states that the species hatch in the spring of the year following ice-out, generally corresponding with mid-March to mid-April (Lawler, 1965; Hoagman, 1973; Freeburg et al., 1990; McKenna and Johnson, 2009).

Larval survival directly influences recruitment and cohort strength, therefore information on factors that affect larval survival allows fisheries managers to forecast future yield using stock-recruitment models (Ricker, 1975). Historically, whitefish larval survival and thus recruitment has been difficult to quantify. Whitefish recruitment is thought to be dependent on abiotic and biotic environmental conditions, in particular, adult population abundance (Lawler, 1965; Taylor et al., 1987; Freeburg et al., 1990; Brown et al., 1993). Of the abiotic factors affecting recruitment, water temperature and ice cover have been the most commonly identified in the whitefish literature (Christie, 1963; Lawler, 1965; Taylor et al., 1987; Freeburg et al., 1990; Brown et al., 1993).

Increased recruitment is attributed to years with fall temperatures less than 6.1 °C prior to spawning, followed by steadily falling temperatures leading into the winter months, and gradual increases in spring temperature leading to larval emergence (Lawler, 1965). Freeburg et al. (1990) indicated that recruitment was influenced by ice cover, suggesting that years with longer periods of ice cover would lead to higher recruitment because of the added protection for eggs from wind-generated wave disturbances. Also, spring water temperature influences the production of zooplankton, which in turn has implications for growth and survival of larval whitefish (Freeburg et al., 1990). Larval whitefish transition from endogenous (yolk sac) to exogenous feeding patterns approximately 3.5 to 4.5 weeks after emergence (Hoagman, 1973); during this critical period larvae begin feeding on zooplankton. Other factors impacting recruitment include predation on larvae and anthropogenic inputs (such as siltation) (Roelofs, 1958; Trautman, 1981; Loftus and Hulsman, 1986; Evans et al., 1996). Predation on whitefish larvae by species such as rainbow smelt (*Osmerus mordax*), alewife (*Alosa pseudoharengus*), and yellow perch (*Perca flavescens*) is common. Loftus and Hulsman (1986) reported that predation by adult rainbow smelt on larval whitefish and lake herring (*Coregonus artedii*) in Twelve Mile Lake, Ontario can be intense because of the coincidence of larval whitefish emergence and peak smelt spawning activity, which corresponds with intensified smelt feeding activity. During this period, average daily consumption rate of larval coregonids per smelt was 8.4. Similarly, Hart (1930) documented that larval whitefish were primary prey items of yellow perch and lake herring when in similar depth strata. Stomachs from 15 yellow perch (~8" TL) contained

3,500 whitefish fry, and stomachs from 12 lake herring (~10" TL) contained 3,300 whitefish fry.

The wide array of factors and annual variability influencing larval survival make recruitment difficult to quantify. Fisheries scientists have attempted to incorporate energy allocation in fish to predict recruitment. Kratzer et al. (2007) attempted to relate the energy content, in the form of egg lipid content, to recruitment/production in whitefish from the Great Lakes, but no decisive relationship was documented. Energy resources within fish are based on prey and energy content of their prey. Following the disappearance of *Diporeia* in many of the Great Lakes, whitefish energy content has decreased, which is expected to negatively impact the reproductive success of whitefish. Hoyle et al. (1999) reported that recruitment of whitefish decreased in Lake Ontario in association with dreissenid invasions and *Diporeia* declines, but studies on whitefish recruitment following dreissenid introductions are limited.

Conclusion

Population assessments focusing on estimating characteristics of fish populations are important for understanding fluctuations in a population over time and add valuable information for managing populations (Van Den Avyle and Hayward, 1999). Whitefish in Lake Champlain have been unstudied in the last ~80 years, and limited information is available on the biological attributes of the population. Limited information on length and age structure, growth, and condition were reported by Van Oosten and Deason (1939). However, given the changes in the whitefish populations within the Great Lakes following the introduction of zebra mussels, it is important determine whether the introduction of zebra mussels has impacted whitefish in Lake Champlain. In addition to

identifying impacts caused by zebra mussels, the information gained through a thorough population assessment will allow for the proper management of whitefish in Lake Champlain.

Chapter 1:

Comparison of Precision and Bias of Scale, Fin Ray, and Otolith Age Estimates for Lake Whitefish (*Coregonus clupeaformis*) in Lake Champlain

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Abstract

We compared the precision, bias, and reader uncertainty of scales, dorsal fin rays, and sagittal otolith age estimates from 151 lake whitefish (*Coregonus clupeaformis*) from Lake Champlain, 2009. Mean and systematic differences in age estimates were compared among structures using consensus ages from two readers; precision of age structures was quantified through the use of age-bias plots, coefficient of variation, and percent agreement; reader confidence was indexed as a measure of overall reader uncertainty for each individual fish by structure. Mean age estimates based on otoliths were systematically higher (7.8 years) than based on scales (6.0 years) or fin rays (5.6 years). Ages determined using otoliths generated a wider range of ages and greater number of age classes (1-23 years, 20 age classes) when compared with scales (1-16 years, 15 age classes) and fin rays (1-14 years, 13 age classes). Otoliths were the most precise of the structures (CV = 4.7, compared with 7.4 for scales and 12.1 for fin rays). Percent agreement between readers indicated high precision and reproducibility of age estimates using otoliths. Percent reader uncertainty was lowest when using otoliths (7.6%) in comparison with fin rays (21.2%) or scales (26.8%). This study is the first evaluation of precision and bias of age structures for Lake Champlain's unexploited lake whitefish population and suggests that otoliths are the most appropriate structure for age estimation. However, the differences in age estimates from the three structures in this study emphasize the importance of validating aging structures to provide accurate age estimates for Lake Champlain.

Introduction

Age data from fish populations are valuable for modeling population dynamics to understand trends in growth, age at maturity, and estimates of mortality (Campana, 2001). The use of inaccurate ages can cause severe errors in fish population management (Beamish and McFarlane, 1983; Yule et al., 2008). Given the importance of accurate estimates of age, in recent years fisheries scientists have focused on the importance of validating and comparing the various aging structures (Mills and Beamish, 1980; Beamish and McFarlane, 1983; Muir et al., 2008a; Bruch et al., 2009; Davis-Foust et al., 2009).

Age estimation has been examined in lake whitefish (*Coregonus clupeaformis*) since the late 1920s, initially using scales; scales are still used for routine lake whitefish (hereafter whitefish) age estimation by some state agencies. The scale method of age estimation and justification as published by Van Oosten (1923, 1929), using scales from whitefish held in the New York Aquarium (an artificial environment) for a known period of time; in this study he determined that annuli were formed annually. However, tagged whitefish in Little Moose Lake, New York, failed to form a scale annulus between marking and recapture (Neth, 1955). Such discrepancies led fisheries professionals to begin to determine precision and accuracy of aging structures, using techniques later described by Campana et al. (1995). Aging using scales, fin rays, and otoliths have been compared for many whitefish populations (unexploited and exploited) to determine precision and evaluate ease of preparation. Scales commonly yield lower ages for whitefish in comparison to estimates from fin ray and/or otoliths (Barnes and Power, 1984; Mills et al., 2005; Hosack, 2007; Muir et al., 2008a). The few studies that compare

fin ray to otolith age estimates reported little to no difference between the age estimates from these two structures (Mills and Chalanchuk, 2004; Muir et al., 2008b). Studies validating aging structures for whitefish are limited; however, Mills and Chalanchuk (2004) and Mills et al. (2004) validated otolith and fin rays for age estimation on unexploited whitefish using mark-recapture and successive removal of fin rays.

Concerns regarding the use of age estimates from structures that are not validated are well known (Beamish and McFarlane, 1983; Campana, 2001). However, validation requires capture and recapture of known-age individuals over multiple years to determine whether an annulus was formed each year following initial age estimation for multiple age classes. Because of the long time frame (years) and labor-intensive field work for validation, managers use other techniques to assess age estimation, such as age structure comparisons. Comparisons among aging structures are valuable because ages determined from different structures taken from an individual fish often do not agree, due to difficulty in identifying the first annulus, clustering of annuli on the edge of the structure, or poor preparation of the structure for aging (Campana, 2001; Mills and Chalanchuk, 2004). Clustering of annuli on the edge of a structure is common among older individuals with slow growth rates. Given that growth is variable among populations, the most precise and accurate aging structures may vary among bodies of water. Age-bias plots and the use of statistical tests such as correlation of variation and/or paired t-tests be used when trying to assess bias (systematic or random) and precision of fish aging structures (Campana et al., 1995).

Lake Champlain's unexploited whitefish population has been unstudied for almost 80 years and nothing is currently known regarding the population's age structure.

The objectives of this study were to 1) compare age estimates from three different structures (scales, fin ray, and otoliths), 2) quantify precision of age estimates for each structure, and 3) quantify reader confidence in age determination for each structure from a relatively unstudied whitefish population from Lake Champlain. Mean and systematic differences in age estimates were compared among structures using consensus ages from two readers; precision of age structures were quantified through the use of age-bias plots and percent agreement; and reader confidence was indexed as a measure of overall reader uncertainty for each individual fish by structure.

Methods

Fish collection & processing.— Whitefish were collected from 28 April through 13 November 2009 in Lake Champlain using a 7.6-m semi-balloon otter trawl (6.4-mm stretched-mesh cod end-liner with a chain footrope) and multiple graded monofilament bottom set gill nets to attempt to collect fish of various size classes (Figure 1.1). Gill nets were 70 m long x 1.8 m deep with one 30.5 m panel of 15.2 cm stretch mesh and four 7.6 m panels of 11.4, 12.7, 14, 15.2 cm stretch mesh, 106.7 m long x 1.8 m deep with seven 15.2 m panels of 7.6, 8.9, 10.2, 11.4, 12.7, 14, 15.2 cm stretch mesh, and 152.4 m long x 1.8 deep with two 76.2 m panels of 10.2, 12.7 cm stretch mesh. Whitefish were sacrificed, measured (TL mm), weighed (nearest g), and three aging structures (scales, fin ray, and sagittal otoliths) were collected from each individual. Scales were removed from the region on the fish located between the posterior end of the dorsal fin and the lateral line, cleaned, dried, and mounted between microscope slides. The first three dorsal fin rays were removed at their bases and placed in scale envelopes to dry. Dried fin rays

were embedded in epoxy covering the proximal joint and base of the ray. The rays were then cut into thin cross sections (~1.0 mm) at approximately a 90° degree angle nearest to the base of the ray using a Buehler low speed Isomet® saw with a diamond wafering blade. Sagittal otoliths were extracted and placed in individually labeled scale envelopes. Otoliths were placed in modeling clay for stability and transversely cut through the nucleus using a dremel tool with a 22.23 x 0.13 mm separating disk (Kingsley North, Inc.). Each otolith half was burned lightly on the cut surface to highlight the annuli, similar to the crack-and-burn technique (Schreiner and Schram, 2001).

Two readers estimated ages from all three structures without access to information on fish size or season collected, to avoid potential bias of interpretation. Scales were examined using a microfiche reader. A scale annulus was defined using the criteria of circuli crowding and “cutting over” described in Beamish and McFarlane (1983) and Muir et al. (2008a). Fin ray age was estimated by viewing the cross section with a dissecting scope at 18-110 magnification using transmitted light. A fin ray annulus was defined as the clear opaque zone or ring between the darker areas on the fin ray, which represent periods of growth (Mills and Beamish, 1980; Mills and Chalanchuk, 2004). Otolith age was estimated by viewing each of the burnt sections under reflected light with the same dissecting scope used for estimation of fin ray age. An otolith annulus was defined as the complete distinct dark ring adjacent to a region of clear opaque growth (Muir et al., 2008a, 2008b). Age estimates using all three structures for each individual were blindly assigned by each reader; in situations of uncertainty a second age estimate was also recorded. Lastly, the two readers decided on a consensus age for each individual fish and structure. Consensus age was determined by comparing initial age estimates

from each reader. If the estimates were equal, that age was used; if age estimates from the two readers differed by one year, the older age was used, and if ages differed by more than one year, the older intermediate age between the initial ages was used for analysis. For example, if reader estimates were 6 and 9 years for scales from the same fish, the consensus age recorded was 8 years. Older ages were assigned as the consensus age to compensate for the tendency for scales to commonly underestimate age (Power, 1978; Mills and Beamish, 1980; Barnes and Power, 1984; Mills and Chalanchuk, 2004; Muir et al., 2008a). The same method was used with fin rays and otoliths to remain consistent.

Data analysis.— Mean consensus ages determined using three aging structures (scales, fin rays, and otoliths) were compared using paired t-tests. Precision and bias were quantified for the three structures using age-bias plots and by comparing percent agreement between readers and structures. Age-bias plots illustrate one age reading against another (reader to reader or structure to structure) and are interpreted through reference to the 1:1 equivalence (Campana et al., 1995). Precision was estimated by calculating the percent agreement between readers for each of the three structures, and calculating the coefficient of variation (CV; Campana et al., 1995). The CV formula for each individual was,

$$CV_j = 100 \times \frac{\sqrt{\frac{\sum_{i=0}^R (X_{ij} - X_j)^2}{R-1}}}{X_j},$$

where R equals the number of times the age of each individual was estimated; X_j equals the mean age estimated for the jth fish, and X_{ij} is the ith age estimate for the jth fish (Chang, 1982). The measure of readability or confidence a reader had in each structure was estimated as percent uncertainty. Percent uncertainty was calculated by averaging the

number of fish to which secondary ages were assigned for each structure. For example, if reader 1 was uncertain about 22 estimated ages and reader 2 was uncertain about 14 estimated ages using scales and the total number of individuals examined was 151, the percent uncertainty for scales would be the total number of uncertainties from reader 1 and 2 (i.e., 36) divided by 302.

Results and Discussion

Age was estimated from scales, fin rays, and otoliths using two readers from 151 whitefish collected in 2009. Mean total length of whitefish was 436 mm (SE = 9.7 mm, range = 135-658 mm; Figure 1.2). Mean age estimates based on otoliths were systematically higher (7.8 years) than based on scales (6.0 years) or fin rays (5.6 years). Mean otolith age was significantly greater than mean scale ($P < 0.001$, $df = 150$) and fin ray age ($P < 0.001$, $df = 150$). Mean scale age was also significantly greater than mean fin ray age ($P < 0.001$, $df = 150$). Ages determined using otoliths generated a wider range of ages and greater number of age classes (1-23 years, 20 age classes) when compared with scales (1-16 years, 15 age classes) and fin rays (1-14 years, 13 age classes; Figure 1.3).

Between-reader bias did not occur when using otoliths, scales, or fin rays for age determination. Age estimated by reader 2 plotted against age estimated by reader 1 did not stray significantly from the equivalence line, indicating unbiased estimates between readers for the same structure (Figure 1.4). Otoliths were the most precise of the structures (CV = 4.7), with the tightest groupings of age estimates along the equivalence line, even for older fish (Figure 1.4). Percent agreement between readers indicated high precision and reproducibility of age estimates using otoliths; the two readers completely

agreed for 62.3% of the fish, and their age estimates were within one year for 94% of the fish. Differences in age estimates between readers never differed by more than two years when using otoliths (Table 1.1). Fin rays and scales were less precise (CV = 7.4 and 12.1), especially for individuals estimated to be ≥ 9 years old (Figure 1.4). Fin ray and scale ages also had a lower percent agreement (56.3 and 45.7%, respectively) between readers and the differences in age estimates between readers were also greater; in two instances, scale ages assigned by readers differed by 7 years (Table 1.1).

Prior studies have emphasized the importance of making comparisons with experienced readers (e.g., 10+ years experience, Mills and Beamish, 1980); however, agencies frequently do not have experienced readers and age estimation is done by seasonal employees. Therefore, we argue that the best structure, in the absence of validation, is one that does not require extensive prior experience to estimate age with the highest confidence and precision. We used percent reader uncertainty to determine reader confidence with each structure. Percent reader uncertainty was lowest when using otoliths (7.6%) in comparison with fin rays (21.2%) or scales (26.8%; Table 1.1). The majority (62.2%) of uncertainties recorded by readers were from individuals greater than 450 mm (TL). Mean total length of fish with secondary ages assigned using otoliths was lower (460 mm) than fin rays (466 mm) and scales (483 mm), indicating that readers had higher confidence estimating age for larger individuals with otoliths. Otoliths give the most reproducible age with the highest level of confidence; therefore, they are particularly valuable when age estimation is done by inexperienced readers. For example, Robillard and Marsden (1996) reported that precision increased based on experience, but precision using otoliths was higher than scales even for the most inexperienced readers.

Otolith age estimates were consistently greater beginning with age 4 and older fish when compared with fin rays and age 7 and older fish when compared with scales (Figure 1.5). Scale age estimates tended to be greater than fin ray ages with the difference beginning at age 7 (Figure 1.5). However, this trend was not as distinct as the differences in ages when comparing otolith ages to fin rays or scales.

Our results indicate that age estimates based on scales, fin rays, and otoliths yield significant differences in mean age for whitefish in Lake Champlain. These results are consistent with the general understanding that scale age estimates are frequently lower than otoliths-based estimates for whitefish (Power, 1978; Barnes and Power, 1984; Mills et al., 2005; Hosack, 2007; Muir et al., 2008a). Similarly, otolith age estimates for yellow perch (*Perca flavescens*) and freshwater drum (*Aplodinotus grunniens*) were regularly greater than estimates using scales (Robillard and Marsden, 1996; Davis-Foust et al., 2009). However, we were surprised to find that our age estimates from fin rays and otoliths differed significantly, which was in contrast to to unexploited whitefish populations in Canada (Mills and Chalanchuk, 2004; Mills et al., 2004). The differences in age estimates from the three structures in this study further emphasize the importance of validating aging structures for different populations throughout the native whitefish range to provide accurate age estimates. Without validation, managers should use caution when deciding which structure should be used when assigning fish age for the use in population modeling.

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population dynamics: lessons learned from a Lake Superior cisco stock. *Trans.*
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Table 1.1.— Percent agreement between two readers for three aging structures (otoliths, fin rays, and scales) from 151 whitefish collected in Lake Champlain, 2009. Percent reader uncertainty is the average number of fish to which secondary age estimates were assigned for each structure and is a measure of reader confidence, with the lowest percent indicating the highest confidence.

Between reader difference (yrs)	Otoliths	Fin rays	Scales
0	62.3	56.3	45.7
± 1	94.0	88.7	75.5
± 2	100	97.4	90.7
± 3		98.7	96.0
± 4		100	97.4
> ± 4			100
% Reader uncertainty	7.6	21.2	26.8

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Figure 1.4.— Age-bias plots comparing age estimates from two readers using three structures (fin rays (top), scales (middle), and otoliths (bottom)) for 151 whitefish collected in Lake Champlain, 2009. Error bars indicate ± 1 SD about the mean age assigned by reader 2 compared with the estimated age assigned by reader 1 for the same individuals. The solid line represents 1:1 equivalence between readers.

Figure 1.5.— Age bias plots comparing estimated ages using three structures (fin rays vs. scales (top), fin rays vs. otoliths (middle), and scales vs. otoliths (bottom)) for 151 whitefish collected in 2009 in Lake Champlain. Error bars indicate ± 1 SD of mean estimated scale to fin ray age, the solid line represents 1:1 equivalence between structures. Note the difference in x and y-axis scale for the top figure.

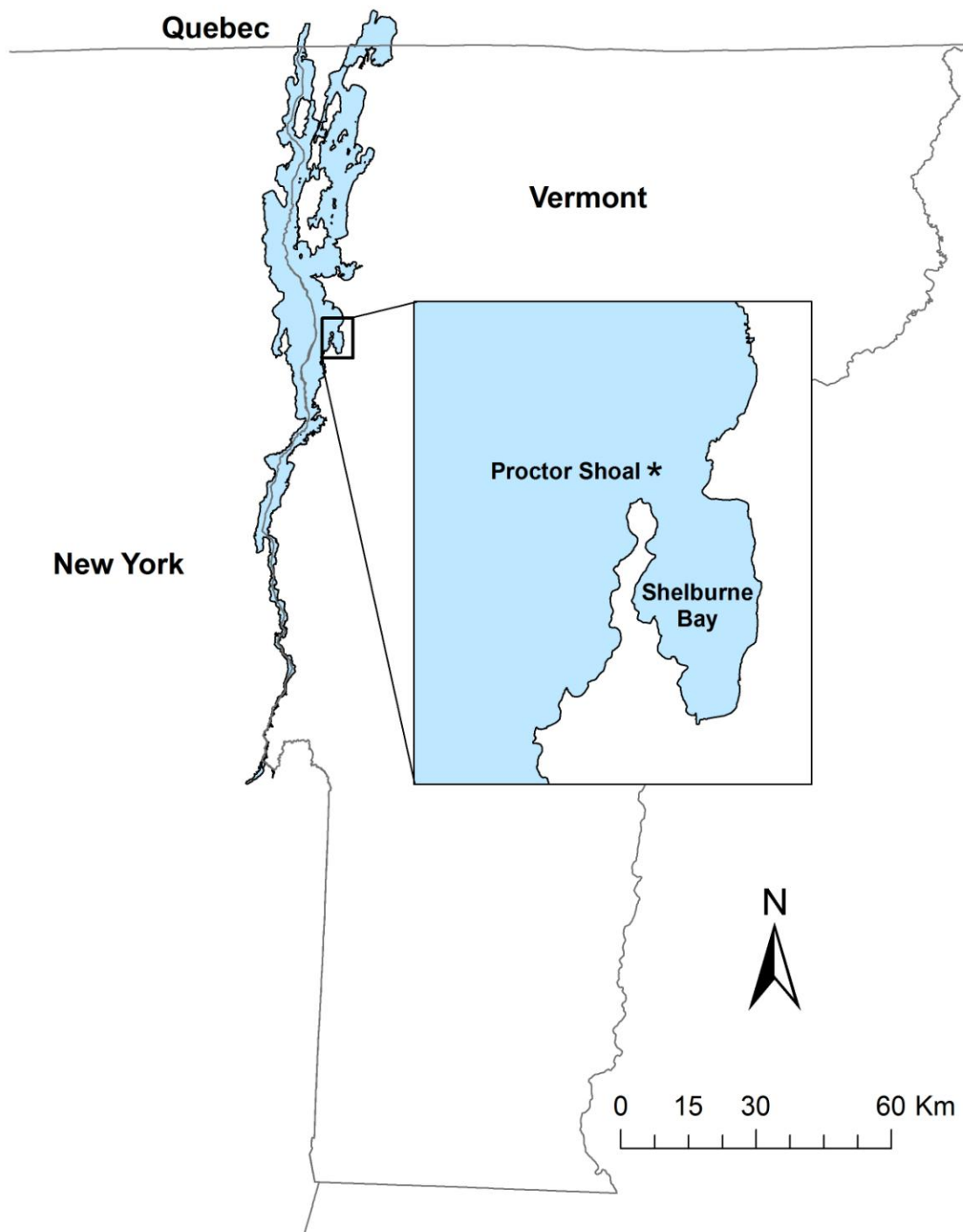


Figure 1.1

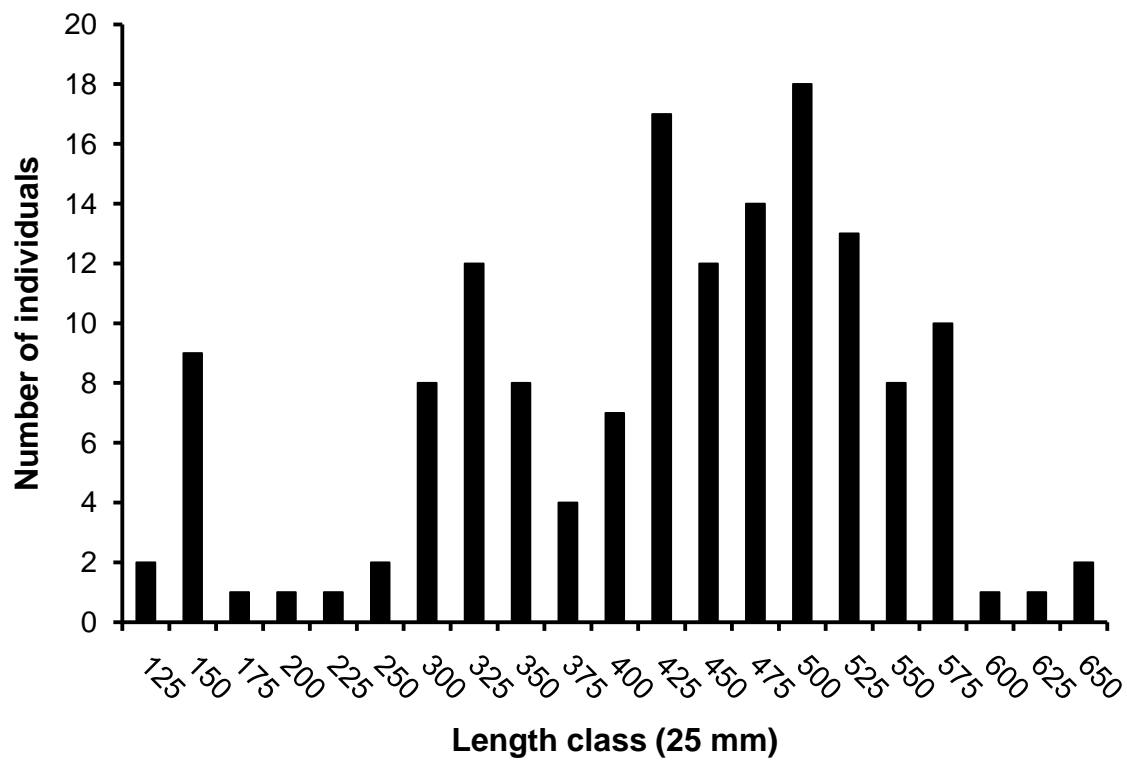


Figure 1.2

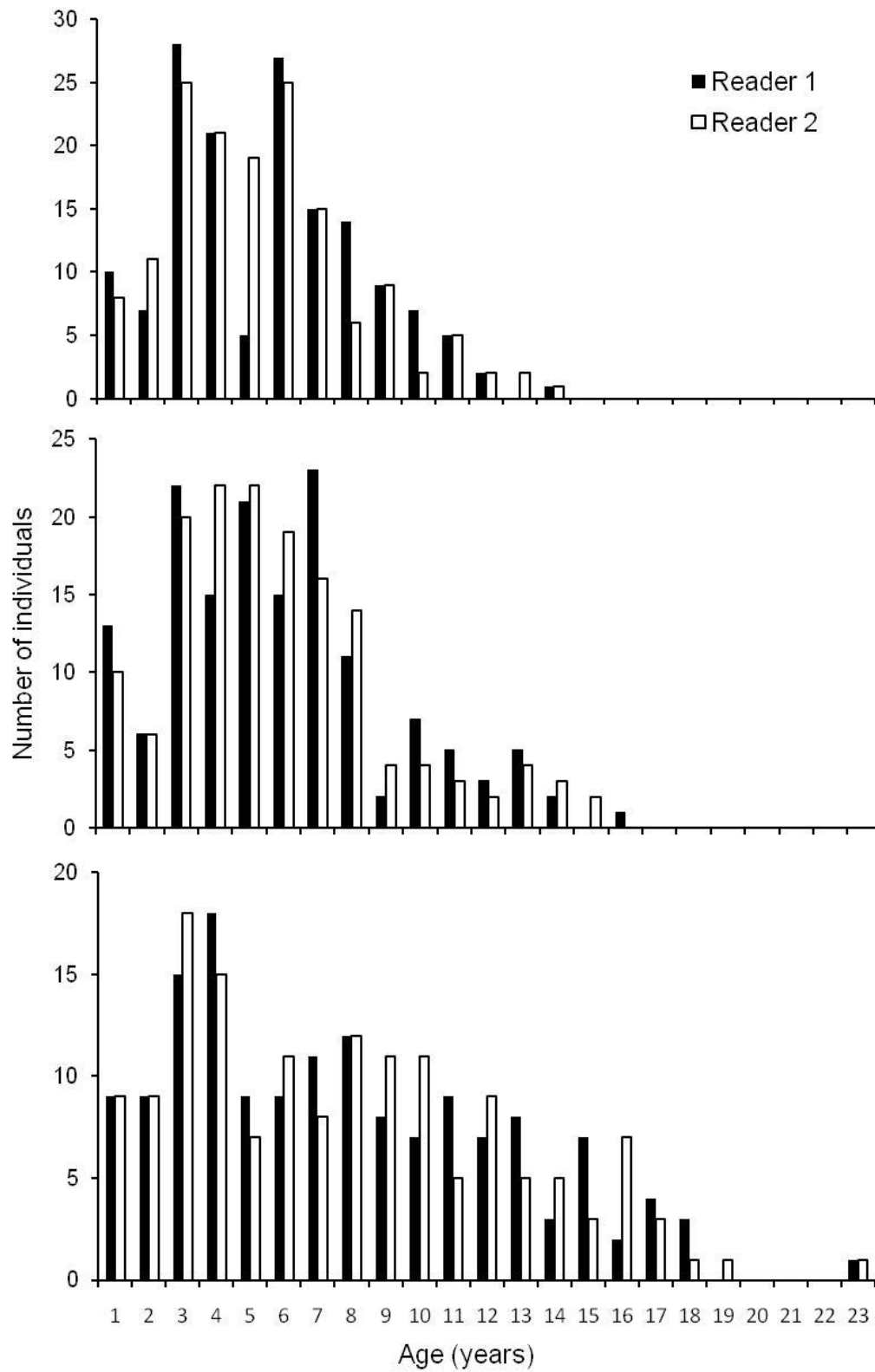


Figure 1.3

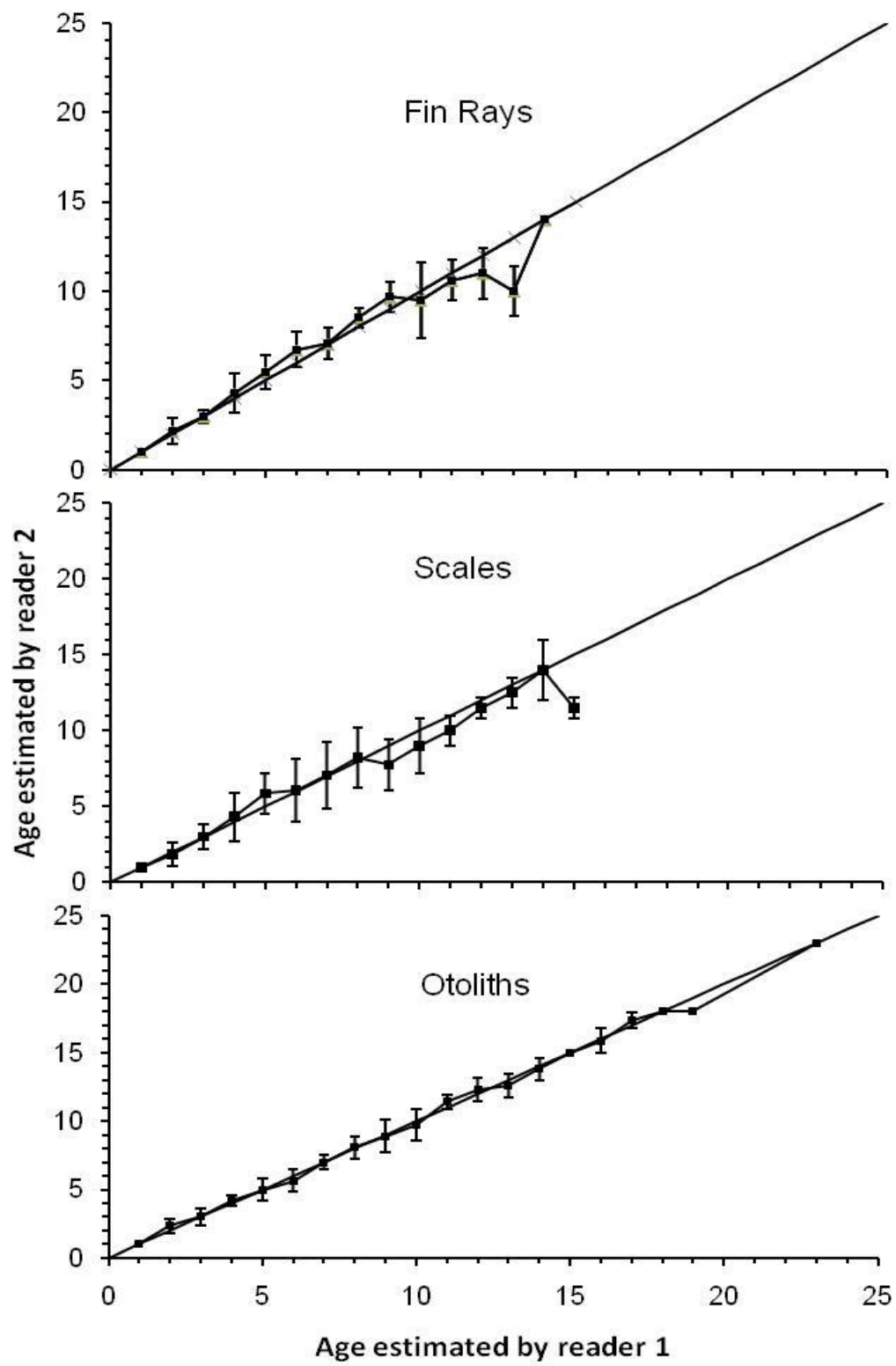


Figure 1.4

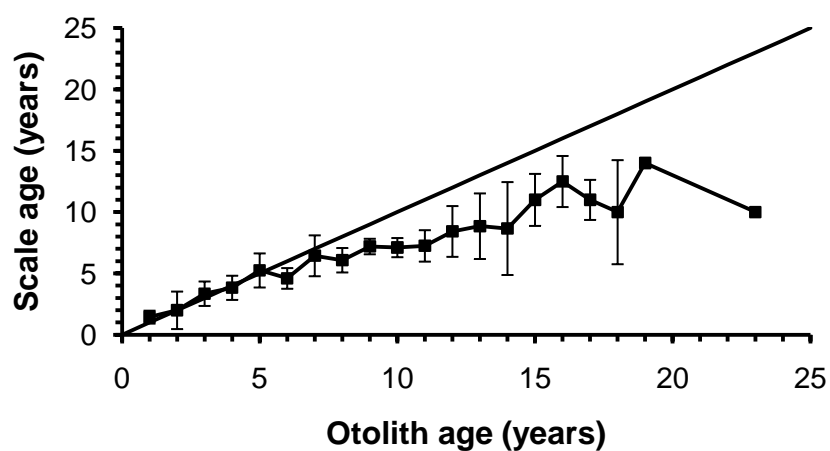
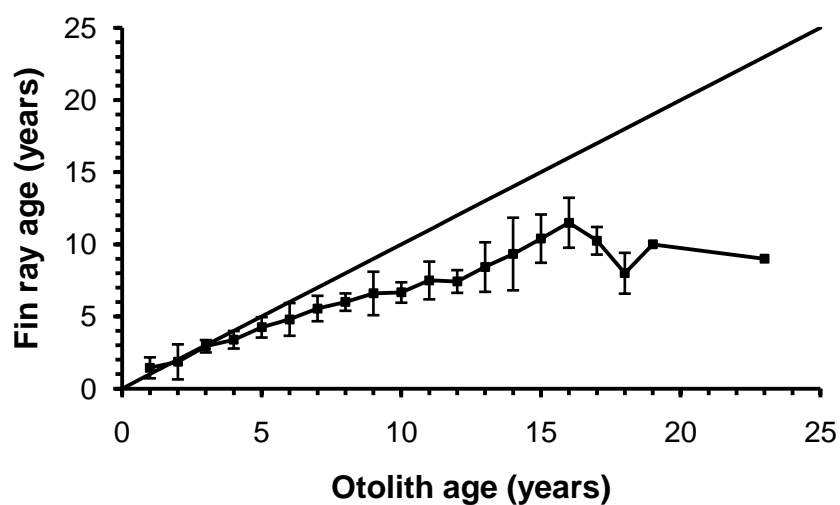
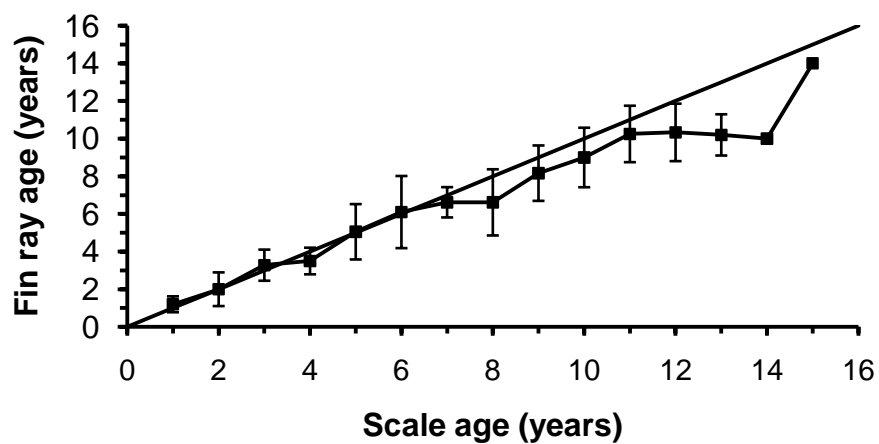


Figure 1.5

Chapter 2:

Population Dynamics of Lake Whitefish in Lake Champlain 2009-2010: 90 Years After Commercial Harvest

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Abstract

Lake whitefish support one of the most valuable freshwater fisheries in North America. Whitefish were commercially fished in Lake Champlain until the 1913 fishery closure in U.S. waters. The only study of whitefish in the lake was done in the 1930s. Our goals were to compare current biological parameters with historical information and determine distribution and spatial differences in larval densities, with an emphasis on locating current spawning grounds, to gain insight on the current whitefish population in Lake Champlain. Adult whitefish ($N = 545$) were collected from 2006 to 2010 using gill nets and trawls focused in the main lake. Larvae were collected extensively lake-wide and intensively at Wilcox Cove and Rockwell Bay using an ichthyoplankton net. Population attributes (size, age, and sex composition, growth, condition, maturity, mortality, and fecundity) were typical of stable unexploited populations with a wide range of length (126-638 mm TL) and age classes (1 to 26 years, based on otolith ages). Whitefish from the main lake had a high condition factor and comparable growth parameters to the whitefish collected in the 1930s. Lake Champlain whitefish growth was sexually dimorphic and had greater asymptotic lengths than generally documented for whitefish, but had lower growth coefficients. Larval whitefish were found at sites throughout the main lake and larval densities were some of the highest recorded for the species ($\text{max} = 2,558 \text{ larvae}/1,000 \text{ m}^3$); however, whitefish were not collected on historic spawning grounds. Whitefish population characteristics in the main lake are characteristic of an unexploited population; however, evidence of spawning is absent, or rare, in portions of their historic range where habitat has been altered.

Introduction

Historically, Lake Champlain supported a thriving commercial shoreline seine fishery in the fall, focused at Missisquoi Bay in the north and Larabee's Point in the south. Overall harvest and license sales peaked from 1895 to 1912. Lake whitefish (*Coregonus clupeaformis*, hereafter, whitefish), were an important part of that commercial fishery. The fishery averaged 68 licenses during that time period and reported its highest whitefish yield of 31,751 kg in 1912, with an average annual whitefish yield of 18,537 kg/year (Halnon, 1963). In the early 1900s, concerns regarding overexploitation of whitefish arose. Fishermen and legislators at the time expressed the opinion that the state of Vermont would obtain greater economic benefits from a strictly recreational fishery; as a result, the commercial harvest was closed in Vermont waters in 1913 (Halnon, 1963; Joint Fisheries Commission 1897). The Quebec whitefish fishery in Missisquoi Bay continued, however, despite substantial decreases in harvest and the number of licenses through time, with only four licensed fishermen harvesting a total of 35 kg in 2004. In 2005, Quebec fishermen voluntarily ceased seining because the high effort associated with netting did not justify the limited harvest (Miller personal comm., 2006).

Since the closure of the commercial whitefish fishery in U.S. waters of Lake Champlain in 1913, only one study has focused on whitefish. In the early 1930s, Van Oosten and Deason (1939) described age and size structure, growth, and condition of whitefish collected in the fall of the year at the two commercially harvested locations within the lake. In more recent years, whitefish have only been recorded as present or absent during biological surveys conducted periodically from the 1930s to the late 1990s.

During the 1970s a fish population inventory documented whitefish in all areas of the lake except for the two historic commercially fished locations (Anderson, 1978). The highest whitefish catch rates were in the main lake. Whitefish were also present in all annual gillnetting surveys from 1982-1998 that were associated with the assessment of lake trout populations before and during the experimental sea lamprey control program (Fisheries Technical Committee, 1999).

Currently, little is known about the biological attributes of whitefish in Lake Champlain. In the 80 years since the 1930 study, Lake Champlain has experienced substantial physical and biological changes. Deforestation during the 1800s, inputs from agricultural land, and shoreline development have led to increased phosphorus loads and eutrophication, especially in the northern and southern portions of the basin (Myer and Gruendling, 1979; Lake Champlain Basin Program, 2008). Exotic species have been entering Lake Champlain at an increasing rate, particularly through the canal system that connects the lake to the Hudson River, Erie Canal, and the Great Lakes. As of 2009, 48 exotic species have colonized the lake; of those invaders alewife (*Alosa pseudoharengus*) and zebra mussels (*Dreissena polymorpha*) have the highest potential to negatively impact the lake's native fish community (Marsden and Hauser, 2009; Marsden et al., 2010). The management goals for whitefish, are to have a population of whitefish with multiple spawning populations, including historical spawning areas that still contain suitable habitat (Marsden et al., 2010). To address these management goals, an analysis about the current status of the species is needed.

Our goals were to describe the population dynamics of whitefish in Lake Champlain almost a century after the closure of the commercial fishery in US waters, and

compare our data with information collected in the 1930s from the two commercially harvested locations. Our objectives were (1) to determine whether changes have occurred in whitefish use of historic spawning grounds and quantify larval densities during emergence in the spring, and (2) quantify whitefish size, age, sex composition, growth, condition, maturity, mortality, and fecundity. Spawning grounds were identified by sampling larvae lake-wide; in particular, use of historic and commercially harvested spawning grounds was identified by the presence or absence of larvae. Peak larval emergence was quantified at two locations using ichthyoplankton nets throughout the hatching period. We estimated growth parameters using the von Bertalanffy growth model, condition using the weight-length relationship, mortality rates using the catch curve equation, and fecundity using the gonadosomatic index (GSI); to compare condition of our whitefish with historic data we used Fulton's K.

Methods

Study Area.— Lake Champlain is a long (~200 km), narrow (~12 km at its widest point), and deep (19.5 m average, 122 m max depth) lake with a surface area of 1,130 km². The lake is bordered by U.S. states of Vermont (east shoreline) and New York (west shoreline), and the Canadian Province of Quebec (north). Lake Champlain flows from southern tributaries north to the northern outlet, the Richelieu River, which flows into the St. Lawrence River. Lake Champlain is comprised of four basins, separated by geographic and constructed barriers, with varying watershed land use (agriculture to forested), trophic status (eutrophic to oligotrophic), fish populations (warm-water to cold-water species), and geology (Myer and Gruendling, 1979). This study focuses on four main areas, the south lake near Larabee's Point, Missisquoi Bay in the north, Proctor

Shoal in the main lake, and the west shore of Grand Isle in the main lake (Figure 2.1).

Two of the study sites (Missisquoi Bay and Larabee's Point) are similar in terms of physical, biological, and chemical characteristics. Both areas are primarily shallow and eutrophic, dominated by a warm-water fish community, and have had historic inputs of phosphorus and sediments from the surrounding land use dominated by agriculture. The main lake, on the other hand, is primarily deep and oligotrophic, supporting warm and cold-water species, and has been less influenced by riparian inputs of phosphorus, contaminants, and sediment (Myer and Gruendling, 1979; Lake Champlain Basin Program, 2008).

Fish collections.— Larval whitefish were sampled in 2008-2010 lake-wide from ice-out until catches declined to zero; this period began as early as April 14 and extended to the first week in June. Larvae were collected using an ichthyoplankton net (75-cm dia opening, 600- μ m mesh) towed on the surface behind a boat at approximately 3.5 km/hr for 10 min during the day; sampling was focused near shore at 2-4 m water depths. Larval whitefish catches were standardized to catch-per-unit-effort and reported as larvae/1,000 m³. Intensive sampling (three tows once a week from mid-April to early June in 2008 and 2009) was done in Rockwell Bay and Wilcox Cove (Figure 2.1) to quantify temporal changes in larval densities. Extensive sampling (single tows during mid-April to early June) was done lake-wide in 2008 and 2009 to determine presence or absence of larvae and distribution of whitefish spawning grounds. Offshore (0.5 to approximately 4 km from shore, depths > 30 m) larval sampling in 2010 was conducted in mid-May west of Wilcox Cove and Rockwell Bay. Sampling was conducted at Wilcox Cove in 2008 to test if larvae concentrations varied at different times of the day; triplicate

samples were collected on one date during the day, at dusk, and an hour after sunset. Samples were placed in 70% ethanol at the field site and taken to the laboratory for measurement and identification. Identification of larval whitefish was confirmed using Auer's (1982) key.

Juvenile and adult whitefish were sampled in the fall of 2006-2008 and year-round during 2009-2010 in the main lake near Proctor Shoal (Figure 2.1). Sampling of adult fish was also conducted in Missisquoi Bay and Larabee's Point in the spring and fall of 2009. Whitefish were collected using a 7.6-m semi-balloon otter trawl with a 6.4-mm stretched-mesh cod-end liner and a chain footrope, primarily targeting juveniles, and bottom-set gill-nets to capture adults. Gill nets were 1.8 m deep and 70.6 to 152.4 m long, and included panels of 7.6, 8.9, 10.2, 11.4, 12.7, 14, and 15.2 cm stretch mesh; we did not use standardized nets due to low catches per net (mean = 2.2 fish/net) and a paucity of historic data for relative CPUE comparisons. Whitefish were weighed (nearest g), measured (total length \pm 1 mm), and examined internally for sex determination. A scale sample was taken from above the lateral line, and otoliths were extracted and stored in labeled envelopes for age estimation; ovaries were removed from females collected in the fall leading up to spawning activity (October-December) during 2006-2009 to estimate fecundity.

Data Analysis

Growth & condition.— Growth was estimated by fitting the von Bertalanffy growth model to mean length at age data to estimate growth model parameters (L_{∞} , K , and t_0) for all whitefish collected from the main lake during 2006 to 2010 (Ricker, 1975):

$$L_t = L_{\infty} * (1 - e^{-k(t-t_0)})$$

where L_t is length at time t , L_∞ is the asymptotic average maximum length, K is the rate at which L_t approaches L_∞ (growth coefficient), and t_0 is the hypothetical age when L_t is zero. Otolith age estimates were used for all whitefish collected during 2006 to 2010 because otoliths were determined to be the least biased and most precise of three aging structures examined for whitefish in Lake Champlain (Chapter 1). Growth parameters from the von Bertalanffy model were estimated separately for each sex (full model) and for both sexes combined (reduced model). Differences in growth between sexes were tested using likelihood ratio tests (Kimura, 1980). Residual sums-of-squares were compared for the full and reduced models using a likelihood ratio test. The full model was accepted if the residual sums-of-squares was significantly different ($P \leq 0.05$) from the reduced model; otherwise, the reduced model was accepted, and the growth parameters for both sexes combined were used. Growth was also estimated separately by including the younger individuals that were classified as unknown sex by adding the unknown fish to both sexes. Differences in growth between sexes with the unknowns included were tested using the same likelihood ratio methods described above.

Growth was also estimated for whitefish collected in 2009 using scale age estimates to compare with historic data from Missisquoi Bay and Larabee's Point (Van Oosten and Deason, 1939). Historic mean standard length (mm) was converted to total length (mm) using a conversion factor ($SL * 1.18$) developed for Lake Champlain whitefish (Van Oosten and Deason, 1939). Differences in growth between all pairwise combinations of locations (Missisquoi Bay, main lake, and Larabee's Point) were tested using likelihood ratio tests (Kimura, 1980). Growth parameters from the von Bertalanffy model were estimated separately for each location (full model; e.g., Missisquoi Bay) and

for each pair of locations (reduced model; e.g., Missisquoi Bay and main lake). Residual sums-of-squares were then compared for the full and reduced models using a likelihood ratio test. The full model was accepted if the residual sums-of-squares was significantly different ($P \leq 0.05$) from the reduced model, otherwise the reduced model was accepted, and the growth parameters for combined locations were used.

Whitefish condition was estimated from all individuals collected during 2006-2010 using the power function (Anderson and Neumann, 1996):

$$W_i = \alpha L_i^\beta$$

where W_i is the weight of the i th fish, α is the condition factor, L_i is length of the i th fish, and β is the shape parameter. To estimate the weight-length parameters (α , and β) from the power function, weight-length data were logarithmically transformed and simple linear regression was used with the following equation:

$$\log_{10}(W_i) = \log_{10}(\alpha) + \beta \log_{10}(L_i)$$

To determine whether body condition differed between males and females, we compared the weight-length relationships between sexes using a general linear model (GLM):

$$\log_{10}(W_i) = \log_{10}(\alpha) + \beta \log_{10}(L_i) + b_1 X + b_2 (X * \log_{10}(L_i)) + \varepsilon_i$$

where X is sex (main effect), $\log_{10}(L_i)$ is the base-10 logarithm of length of the i th fish, and other terms are defined as for the power function. The homogeneity of slopes between sexes was tested using the interaction between sex (main effect) and the covariate. Separate sex-specific weight-length models were used if the interaction between \log_{10} length and sex (b_2) was significant ($P < 0.05$). Because the interaction term was not significant, the interaction term was removed and the reduced model was used; separate weight-length models were fitted to each sex. A final separate weight-length

model was used to incorporate the unknown sex individuals to estimate condition parameters for all fish collected in the main lake during 2006-2010.

Whitefish condition was estimated from individuals collected in the fall using Fulton's K condition factor (Anderson and Neumann, 1996):

$$K = \frac{W}{L^3} * 100,000$$

to compare with values estimated for each sex from whitefish collected in 1930 and 1931 (Van Oosten and Deason, 1939). This technique was used for historical comparison because the original weight-length data from Van Oosten and Deason (1939) were not available. Instead, historic condition was only reported as mean condition value (Fulton's K) by sex using standard length (mm), so our length data were converted to standard length for this comparison using (SL = TL * 0.845) (Van Oosten and Deason, 1939). Differences in body condition, by sex, of individuals collected from 2006-2010 in the main lake and the two historic locations (Missisquoi Bay and Larabee's Point) were examined using the 95% confidence intervals from main lake fish to determine whether condition values overlapped.

Maturity. — Sex was determined by internal examination of reproductive organs during all seasons. Male or female classification did not necessarily mean that the individual was sexually mature and ready to spawn in that year. The inability to determine whether a fish of either sex had or was about to spawn made it impossible to estimate the age at which 50% of the population reached maturity. Instead, we define maturity as the age at which the individuals sampled started to have identifiable reproductive organs, and realize that this age is almost certainly lower than true maturity.

Mortality. — Mortality rates were estimated for whitefish collected in the main lake during 2006-2010 using the catch curve analysis equation (Ricker, 1975):

$$N_t = N_o e^{-Zt}$$

where N_t is the number present at age t , N_o is the average annual recruitment, Z is the instantaneous total mortality rate, and t is the age of fully recruited fish. To determine the age at which fish were fully recruited, we visually examined the histogram of natural log of catch with age and chose the age that corresponded to the peak leading to the descending limb of the distribution. We \log_e -transformed the catch curve equation to estimate Z using linear regression of $\log_e(N_t)$ against age t beginning with the first fully recruited age:

$$\log_e(N_t) = \log_e(N_o) - Zt$$

where the slope of the model is the instantaneous total mortality rate (Z). Annual mortality rate (A) was then calculated as:

$$A = 1 - e^{-Z}.$$

Fecundity. — Ovaries were extracted, weighed (total weight, nearest 0.1g), and three subsamples of eggs were removed, discarding any ovarian tissue within the sample. Subsamples (approximately 1 g) were weighed and eggs were counted. Egg counts were then extrapolated to estimate the number of eggs per whole ovary and estimate the relationship between fecundity and fish weight. The gonadosomatic index ($GSI = \text{ovary weight/body weight}$) was used to determine the proportion of ovary weight to body weight of adult female whitefish (Strange, 1996). Total length (mm) was used as a predictor of fecundity using a power function with $\log(\text{fecundity})$ as the dependent variable and $\log(\text{length})$ as the independent variable.

Results

Larval collections

In 2008-2009, larval whitefish were distributed throughout the main lake (Figure 2.2). Larval whitefish were present at all locations sampled within the main lake, but were found in very low numbers and at only one location in the Inland Sea (Figure 2.2). Larval whitefish were also sparse in samples from the historic commercially fished location, Larabee's Point, with a maximum daily average density of 5 larvae/1,000 m³ from nine sample days, 2008-2010 (Figure 2.2). In contrast, the maximum daily average at Wilcox Cove was 2,558 larvae/1,000 m³. Larval tows in Missisquoi Bay, the other historic commercially fished location, yielded no whitefish larvae collected in any of the three sampling years. The highest densities of larval whitefish were associated with shoreline habitats consisting of cobble/gravel substrate as opposed to areas heavily dominated by habitats with wetland characteristics (highly organic substrate and high macrophyte densities). Larval whitefish were also present in all exploratory offshore samples. At Wilcox Bay the highest densities of larvae were collected at dusk (1,583/1,000 m³) compared to 961/1,000 m³ during the day and 218/1,000 m³ after sunset of the same day.

Intensive larval sampling conducted at Wilcox Cove and Rockwell Bay during 2009 captured peak larval emergence densities of 2,558 and 2,244 larvae/1,000 m³, respectively (Figure 2.3). Larval emergence at the two locations began to rapidly increase on approximately 8 May 2009, which corresponded with water temperatures ranging from 7.8 - 9.4 °C, and declined sharply following the peak at both locations (Figure 2.3).

Total length of larval whitefish at the two locations ranged from 10 mm on 22 April to 17 mm on 3 June 2009.

Adult distribution, size, age & sex composition

A total of 545 whitefish were collected in gill nets and bottom trawls conducted from 25 November 2006 to 6 October 2010. Gill nets set in the main lake captured 464 whitefish (mean = 0.72 fish/hr) with a mean total length of 496 mm (SE = 3.47, range = 240-658 mm) and a mean total weight of 1,409 g (SE = 642, range = 100-3,300 g). Gill nets set in Missisquoi Bay and Larabee's Point captured nine whitefish (mean = 0.19 fish/hr), all of which were collected at the southern entrance of Missisquoi Bay during November. The bottom trawl captured 81 whitefish with a mean total length of 301 mm (SE = 11.20, range = 126-511 mm) and a mean total weight of 377 g (SE = 40, range = 14-1,540 g). Overall, whitefish captured in both gears had a mean total length of 467 mm (SE = 4.51, range = 126-658 mm) and a mean total weight of 1,256 g (SE = 30.48, range = 14-3,300 g; Figure 2.4). The sex composition, determined from 346 whitefish, was slightly skewed toward females (females = 0.55; males = 0.45).

The age-frequency distribution indicates that multiple age classes were sampled in the main lake during 2006-2010. Age groups ranged from age 1 to 26 with a mean age of approximately 9 years (SE = 0.20) based on otolith age estimates (Figure 2.5). The use of the bottom trawl increased our sample size of younger individuals; of the 79 fish aged captured in the trawl, 70% were age-3 or younger.

Growth and condition

Whitefish collected from the main lake during 2006-10 exhibited sexually dimorphic growth. Female and male growth parameters using mean length at otolith age

differed significantly ($P = 0.02$). Females achieved larger asymptotic total lengths than males ($L_{\infty} = 637$ mm vs. 604 mm; Figure 2.6). Growth coefficients (K) were similar between the two sexes with the males having a slightly larger growth rate ($K = 0.14$ vs. 0.11). Asymptotic total lengths decreased with the inclusion of the unknown sex individuals ($L_{\infty} = 598$ mm) in the growth model, but the growth coefficient K ($K = 0.20$) was higher compared with the growth models for either sex (Figure 2.6). The length at age 0 (t_0) increased from -5.40 (males only) and -3.17 (females only) to -0.81 with the younger, unknown sex fish included in the growth model.

Whitefish growth estimated from a subset of 219 individuals using scale age estimates collected from the main lake during 2009 was not significantly different from historic whitefish growth estimated from 175 Larabee's Point ($P = 0.06$) or 120 Missisquoi Bay whitefish ($P = 0.147$). Missisquoi Bay and Larabee's Point whitefish had significantly different growth parameters ($P = 0.012$) (Van Oosten and Deason 1939). Missisquoi Bay whitefish collected in 1930 attained the largest asymptotic length ($L_{\infty} = 635$ mm) compared with Larabee's Point ($L_{\infty} = 607$ mm) and our main lake fish ($L_{\infty} = 605$ mm). Growth coefficient (K) decreased from south (Larabee's Point $K = 0.28$) to north (Missisquoi Bay $K = 0.21$) with our centrally located main lake site having an intermediate value ($K = 0.24$; Figure 2.7).

Male whitefish had a significantly larger mean condition factor than females ($\alpha = 1.58E-6$ vs. $7.91E-7$; $P < 0.01$), but there was no difference in shape parameters (β : females = 3.42, males = 3.30; $P = 0.13$). When the unknown sexed individuals were included with males and females combined, the shape parameter was the lowest of all three models ($\beta = 3.22$), but whitefish still exhibited allometric growth ($\beta > 3.0$). The

overall (combined sexes and unknowns) weight-length model described the highest percent (98%) of the variation in weight as a function of length (Figure 2.8), whereas the males-only model described 94% and the females-only model described 95% of the variation in weight as a function in length (Figure 2.8).

Body condition of main lake whitefish estimated using Fulton's K was significantly higher than for whitefish collected from Missisquoi Bay in 1930 for both sexes, but was not significantly different for fish captured at Larabee's Point in 1931 based on the 95% confidence intervals (CI). This comparison with historic data included only the 170 whitefish collected from the main lake in the fall of 2006-2010. Females accounted for 60% of the total main lake sample size and had a greater mean standard length but smaller size range (453 mm; N = 102; SE = 4.49; range = 341-544 mm) than males (444 mm; N = 68; SE = 5.32; range = 276-556 mm). Female whitefish condition ($K = 1.87$; 95% CI = 1.83-1.91) was significantly higher than males ($K = 1.74$; 95% CI = 1.68-1.78) based on 95% CI for fish collected in the main lake. When comparing condition between locations and sexes, females from the main lake ($K = 1.87$) were similar to females from Larabee's Point ($K = 1.84$; N = 77; range = 350-549 mm SL), and both locations had higher condition values compared with Missisquoi Bay ($K = 1.69$; N = 59; range = 350-529 mm SL). The same pattern held true when estimating condition for males; the main lake ($K = 1.74$) was similar to Larabee's Point ($K = 1.71$; N = 98; range = 310-559 mm SL) and significantly higher than Missisquoi Bay fish ($K = 1.62$; N = 61; range = 300 mm SL). Condition values by sex for the fish collected in the main lake during 2006-2010, using total length, showed the same pattern, with females having

higher condition than males. When sexes were combined overall condition decreased but was still above 1.0 (females: $K = 1.13$; males: $K = 1.05$).

Maturity

Reproductive organs were visually identifiable for all individuals from the main lake by age 7 in all years. Maturation is likely to begin between age 3 (12% known sex) and age 4 (72% known sex).

Mortality

Mortality rates were estimated for age 6 and older whitefish collected from the main lake in 2006-2010; based on the age-frequency histogram, whitefish were fully recruited to our gear by age 6 (Figure 2.5). Instantaneous total mortality (Z) for age 6 to age 26 whitefish was estimated at 0.24, annual mortality rate (A) was 0.21, and annual survival rate (S) was 0.79.

Fecundity

Fecundity was estimated from 51 whitefish collected during late September to mid-November, 2006-2009. These whitefish had a mean total length of 524 mm ($SE = 7.49$ mm, range = 419-644 mm) and a mean total weight of 1,760 g ($SE = 87.27$ g, range = 710-3,300 g). Fecundity estimates averaged 43,975 eggs ($SE = 2,330.68$, range = 14,228-85,154 eggs); the mean number of eggs per g of body weight was 197 ($SE = 8.53$, range = 122-386). The mean GSI (gonadosomatic index *100) was 13.9 ($SE = 0.60$, range = 4.38-22.76). Total length (mm) was a good predictor of fecundity, explaining 71% of the variation in fecundity (Figure 2.9).

Discussion

Whitefish in Lake Champlain had biological attributes that were distinctive of an unexploited population. Lake Champlain's whitefish population was represented by multiple age classes and a wide distribution of lengths with multiple modes in the length frequency, consistent with findings from 12 unexploited whitefish populations in Canadian lakes (Mills et al., 2005). Growth and mortality rates for whitefish in Lake Champlain were also representative of an unexploited population with slow growth and low mortality rates.

Larval whitefish were found throughout the main lake, but were scarce or absent in the Inland Sea, Missisquoi Bay, and Larabee's Point. Lake Champlain's shorelines throughout much of the main lake consist of gravel and cobble, which is suitable and preferred spawning substrate for whitefish (Bégout Anras et al., 1999). Prior to this study, knowledge of whitefish spawning grounds in Lake Champlain was limited to historical informational regarding the fall shoreline seining fishery that harvested whitefish in northern (Missisquoi Bay) and southern (Larabee's Point) locations of the lake when the species was preparing to spawn. Larval densities within areas of Lake Champlain are among the highest reported for the species. For perspective, average maximum larval densities in Wilcox Cove and Rockwell Bay (2,558 and 2,244 larvae/1,000 m³) were substantially higher than in Chaumont Bay, Lake Ontario (469/1,000 m³) and Grand Traverse Bay, Lake Michigan (71/1,000 m³), but lower than Green Bay, Lake Michigan (3,756/1,000 m³) (Hoagman, 1973; Freeburg et al., 1990; McKenna and Johnson, 2009). Wilcox Cove and Rockwell Bay have spawning substrate suitable for whitefish and are protected from wave-generated disturbances, except from the west, which can affect egg

survival rates and recruitment. Both bays freeze over early in the winter, and the entire lake is 90-100% ice-covered in most years (Lake Champlain Basin Program, 2010). Freeburg et al. (1990) indicated that recruitment was influenced by ice cover, suggesting that years with longer periods of ice cover would lead to higher recruitment because of the added protection for eggs from wind-generated wave disturbances.

Larval whitefish concentrate at the surface in shallow depths (< 3 m) and are seldom captured over adjacent deep water further from shore after hatching (Hart, 1930; Hoagman, 1973). Our geographically extensive larval sampling in Lake Champlain found mean daily maximum larvae densities of 74/1,000 m³ at the surface over depths ranging from 26-61 m, which is lower than the 449/1,000 m³ captured nearshore, but still substantially higher than central Green Bay where few to zero larvae were captured at offshore sites (Hoagman, 1973). These offshore larvae were presumably displaced from nearshore areas by currents or offshore winds. Night-time larval catches have been reported to yield more whitefish than day-time tows (Hoagman, 1973); however, we collected the highest densities at dusk, and higher densities during the day than at night. These results indicate that larvae in Lake Champlain are found at a range of distances from shore and can be captured in varying densities at different times of the day, thus illustrating the importance of multiple sampling techniques to gain an understanding of the variations in distribution and behavior of the same species for different water bodies.

Despite high larval densities within the main lake of Lake Champlain, larval whitefish were absent (Missisquoi Bay) and rare (Larabee's Pt.) at the two locations that were historically commercially fished. Limited gillnetting also failed to catch many whitefish in Missisquoi Bay. These two locations have been affected by anthropogenic

changes and are now highly eutrophic with high densities of macrophytes and organic matter that limit available oxygen needed for egg survival (Myer and Gruendling, 1979; Lake Champlain Basin Program, 2008). Habitat changes have changed the spawning substrates by covering them with silt and vegetation; similar effects have been shown to negatively influence whitefish recruitment in other systems (Evans et al., 1996).

Whitefish in Lake Champlain had a wide size range with multiple length modes, and multiple age classes, similar to unexploited populations from several Canadian lakes (Johnson, 1976; Mills et al., 2005). In contrast, exploited whitefish populations are characterized by smaller individuals with few older individuals. Sex composition of whitefish in Lake Champlain was slightly skewed toward females; reproductive organs were identifiable by sex by age 3 and all fish were of known sex by age 7. Unexploited fish populations are usually characterized by late maturation, though age at maturity generally varies among populations. Unexploited whitefish in Lake Pend Oreille, Idaho had a sex composition that was slightly skewed toward females; however, age at maturity ranged from 4 to 12 years (Hosack, 2007), whereas all of Lake Champlain whitefish were mature by age 7. In general, males mature as early as the end of their second year of life (Van Oosten and Hile, 1949), but more commonly maturity ranges from 3 to 8 years old and females from 4 to 8 years old (Beauchamp et al., 2004; Hosack, 2007; Lumb et al., 2007). Whitefish experiencing higher exploitation rates compensate for the increased exploitation by increasing growth rates, which often results in earlier maturation (Healey, 1975, 1980), so we expected an older age at maturity from our unexploited population. However, the younger age at maturity in Lake Champlain may be related to our methodology of classifying all individuals of known sex as mature, which probably

underestimated the age at maturity because not all individuals with identifiable reproductive organs may have been mature.

Growth of whitefish from Lake Champlain was sexually dimorphic, with females reaching larger asymptotic lengths and males having greater growth coefficients. Whitefish growth frequently differs by sex in both unexploited and exploited lakes (Beauchamp et al., 2004; Cook et al., 2005; Hosack, 2007). Whitefish from Lake Champlain had an asymptotic length for both sexes (females: 637 mm; males: 604 mm TL) that was greater than exploited Lake Erie whitefish (females: 593 mm; males: 576 mm TL; Cook et al., 2005), unexploited Lake Pend Oreille whitefish, (females: 532 mm; males: 495 mm TL; Hosack, 2007), 22 Great Lakes exploited stocks (females: 596 mm; males: 572 mm TL; Beauchamp et al., 2004), and 28 inland lake populations (females: 558 mm; males: 544 mm TL; Beauchamp et al., 2004); only whitefish from Lake Superior's Apostle Island region had a large asymptotic length (728 mm TL; Seider and Schram, in review). Growth coefficients (K) by sex from Lake Champlain were similar to Lake Pend Oreille (females: 0.13; males: 0.15; Hosack, 2007), but lower than most other whitefish populations. Lake Erie males had a K of 0.32, which was amongst the highest reported; other K values range from 0.22 to 0.31 for Lake Erie females, 28 inland lakes populations, and 22 Great Lakes stocks (Beauchamp et al., 2004; Cook et al., 2005). Growth differences in whitefish between Lake Champlain and other lakes could be the result of many factors. Changes in whitefish growth have been related to density-dependent factors, with slow growth in years of increased abundance and biomass (Healey, 1980; Wright and Ebener, 2005). Abundance and biomass of whitefish in Lake Champlain is unknown, but given the high asymptotic lengths and slow growth rates, we

speculate that density-dependent factors are not limiting growth in Lake Champlain whitefish.

Whitefish from Lake Champlain grew plumper with increases in length, which is typical of whitefish populations. Shape parameters for exploited and unexploited whitefish populations are similar, ranging from 3.04 to 3.69, consistent with our findings (Kennedy, 1953; Healey, 1975). Condition, much like growth, is dependent on food source and metabolic costs (Ney, 1999). Whitefish in exploited systems would be expected to be heavier for their given length in comparison to whitefish from unexploited systems because the stress from intra-specific competition would be alleviated. However, intra-specific competition is a less important factor in determining size in systems that have a sufficient food supply, which could explain the overlap in condition between exploited and unexploited whitefish populations.

Fecundity of whitefish in Lake Champlain was lower (13.9%) than for exploited populations in Lake Erie and Lake Ontario (20.4% and 17.3%, respectively), based on the gonadosomatic index (GSI) (Lumb et al., 2007). In other studies, fecundity estimates have varied with total egg count ranging from 18,433 to 58,567 in two Canadian lakes, comparable to Lake Champlain's mean fecundity of 43,975 (Lawler, 1961; Christie, 1963; Cucin and Regier., 1965; Healey and Dietz, 1984). Variations in fecundity can be caused by many factors, particularly differences in available energy resources. Available energy resources for whitefish populations are often related to density-dependent factors, and can impact the population dynamics. Similar to growth and condition, fecundity is impacted by population density. Kratzer et al., (2007) found that fecundity and whitefish abundance were inversely related at five locations within Lake Michigan. Whitefish

densities in Lake Champlain do not seem to be hindering the population's ability to find available food resources for somatic growth or reproduction; however, following the introduction of zebra mussels (*Dreissena polymorpha*) to Lake Champlain in 1993 (Marsden and Hauser, 2009), we anticipated a diet shifts from native prey to these less energetically valuable exotic mussels, as was seen in the Great Lakes (Mohr and Nalepa, 2005). In the Great Lakes this diet shift negatively impacted growth and condition which ultimately has impacts on reproductive capabilities of a fish population; however, because of the growth and condition values in Lake Champlain whitefish we do not anticipate that similar dietary shifts have occurred in Lake Champlain following the introduction of zebra mussels.

Whitefish from Lake Champlain have been exposed to very little exploitation since the closure of the commercial fishery in U.S. waters in 1912, which can explain the high annual survival rate of 79%, typical for unexploited populations. Mills et al. (2005) summarized 12 unexploited populations of whitefish from Canadian lakes and reported annual survival rates that ranged from 74% to 85%, based on catch curve analysis. Low mortality rates in Lake Champlain whitefish are distinctive of unexploited populations that have large numbers of old individuals and are characteristic of stable populations (Healey, 1975). Exploited populations, on the other hand, are less stable because of low adult abundance; this makes populations susceptible to declines from failures in recruitment, which is highly variable for the species (Lawler, 1965; Taylor et al., 1987; Brown et al., 1993).

The main lake whitefish from our study had similar growth parameters and comparable mean condition values compared to the 1930s fish from Larabee's Point and

Missisquoi Bay, with the one exception that main lake fish had a greater condition value than fish from Missisquoi Bay. Van Oosten and Deason (1939) concluded that Missisquoi Bay and Larabee's Point had separate whitefish populations based on the biological attributes of the fish they collected in the 1930s. However, both of these areas are shallow and too thermally restrictive to support whitefish in the summer; they must only have been used by whitefish for spawning and early larval growth. Given the virtual absence of larvae and adults in our study, we suggest that whitefish spawning no longer occurs in Missisquoi Bay and Larabee's Point. VandeHey et al. (2009) found that whitefish in Lake Michigan have small home ranges and genetically differentiated sub-populations; if similar population sub-structuring was historically present in Lake Champlain, then habitat changes may have eliminated the northern and southern spawning populations. If the whitefish population is panmictic, fish that historically spawned in Missisquoi Bay and at Larabee's Point would now be spawning in the main lake; this would explain the similarities between historic and current growth and condition among all locations. Growth and condition are affected by multiple factors and the differences in the spatial and temporal scales almost certainly biased our comparisons, but we propose that the main lake whitefish population parameters are representative of historic whitefish populations.

Biological attributes of Lake Champlain whitefish are similar to other unexploited whitefish populations throughout their range. The main lake has suitable spawning substrate and some of the highest larval densities reported for the species, which likely indicates that recruitment is not a bottleneck for the population's expansion. Growth and condition are characteristic of an unexploited population and we suggest that whitefish in

Lake Champlain are not affected by density-dependent factors; we would, however, anticipate increases in growth rates if exploitation increased. However, our data indicate that discrete spawning stocks of whitefish have potentially been extirpated from the two commercially fished locations of the lake, likely as a result of historical changes in riparian land use and increased inputs of phosphorus. High sediment loads and phosphorus inputs may have resulted in irreversible changes at Missisquoi Bay and Larabee's Point such that these sites may no longer be suitable for whitefish spawning.

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List of Figures

Figure 2.1.— Map of Lake Champlain with enlarged areas showing study sites. Study sites were Missisquoi Bay (north lake), the main lake (Wilcox Cove, WC, and Rockwell Bay, RB; Proctor Shoal, PS, and Shelburne Bay), and south lake (Larabee's Point, LP).

Figure 2.2.— Larval whitefish sampling locations in Lake Champlain, 2008-2010 (presence = solid circle, absence = cross). Intensive sampling locations (Wilcox Cove and Rockwell) and locations of special concern (Missisquoi Bay and Larabee's Point) are enlarged with the maximum average larval densities \pm SD. The number of sample days is given in parentheses for each year; 3 to 12 samples were taken on each sampling date.

Figure 2.3.— Larval lake whitefish densities (mean number of larvae/1,000m³ \pm SD) during 2009 at Rockwell Bay (top) and Wilcox Cove (bottom), Lake Champlain.

Figure 2.4.— Length frequency of 545 lake whitefish collected during 2006-2010 from Lake Champlain.

Figure 2.5.— Age frequency of 542 lake whitefish collected during 2006-2010 from Lake Champlain.

Figure 2.6.— Predicted mean total length (mm) at age (years) for male (top), female (middle), and all whitefish (bottom) collected in Lake Champlain during 2006-10, using the von Bertalanffy growth model. Error bars indicate \pm 1 SD.

Figure 2.7.— Predicted mean total length (mm) at age (from scale age estimates) using the von Bertalanffy growth model for whitefish collected from Missisquoi Bay in 1930 (N=120), Larabee's Point in 1931 (N=175), and the main lake in 2009 (N=170) (error bars indicate \pm SD). Historical length-at-age data for Missisquoi Bay and Larabee's Point were derived from Van Oosten and Deason (1939).

Figure 2.8.— Weight-length relationship for males (top), females (middle), and all whitefish (bottom) collected from Lake Champlain, 2006-10.

Figure 2.9.— Fecundity by length (mm) for whitefish from Lake Champlain, 2006-2009.

Fecundity = $0.00003 * (\text{length}^{3.3831})$, (F = 123.35.0; df = 1,49; P<0.001).

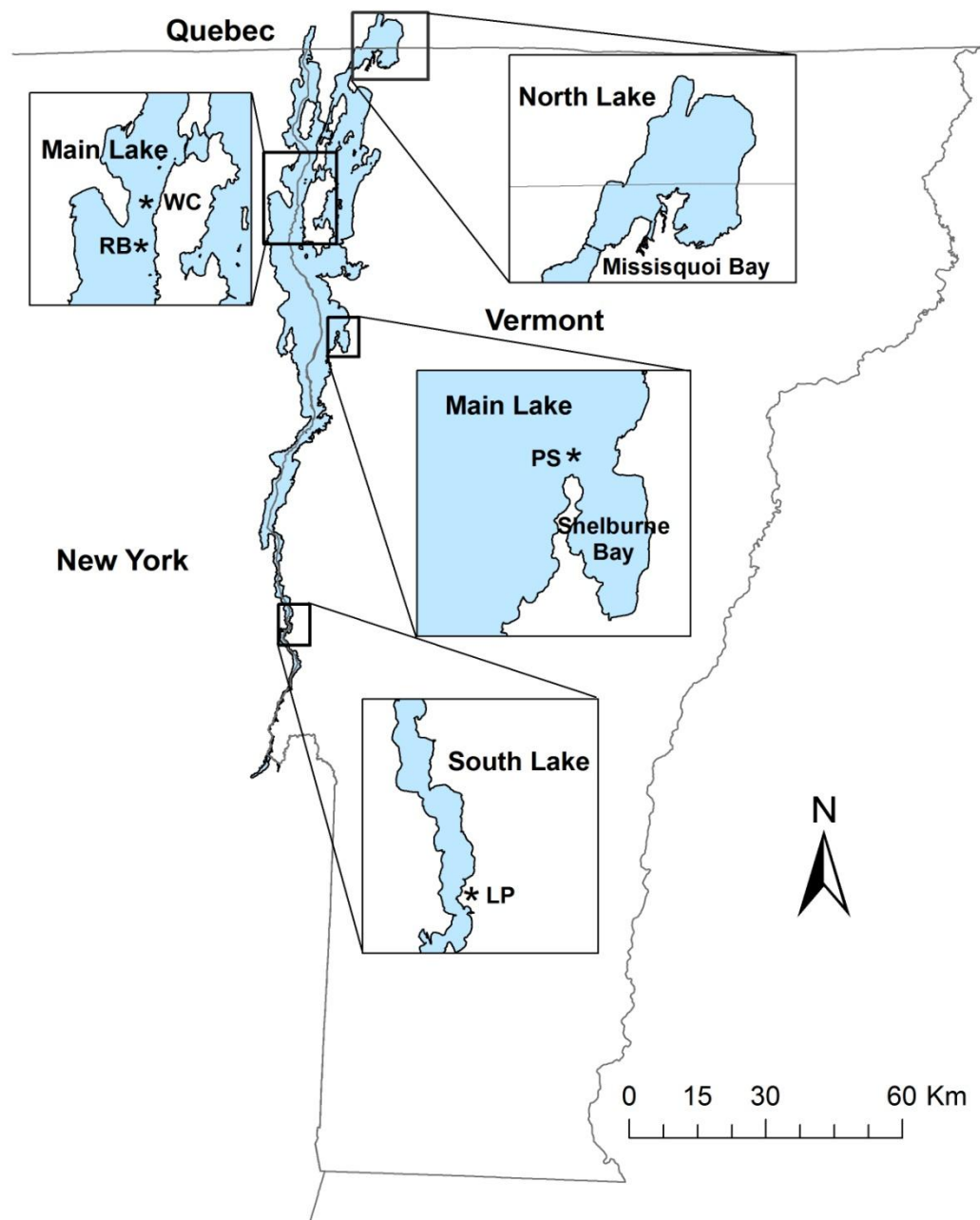


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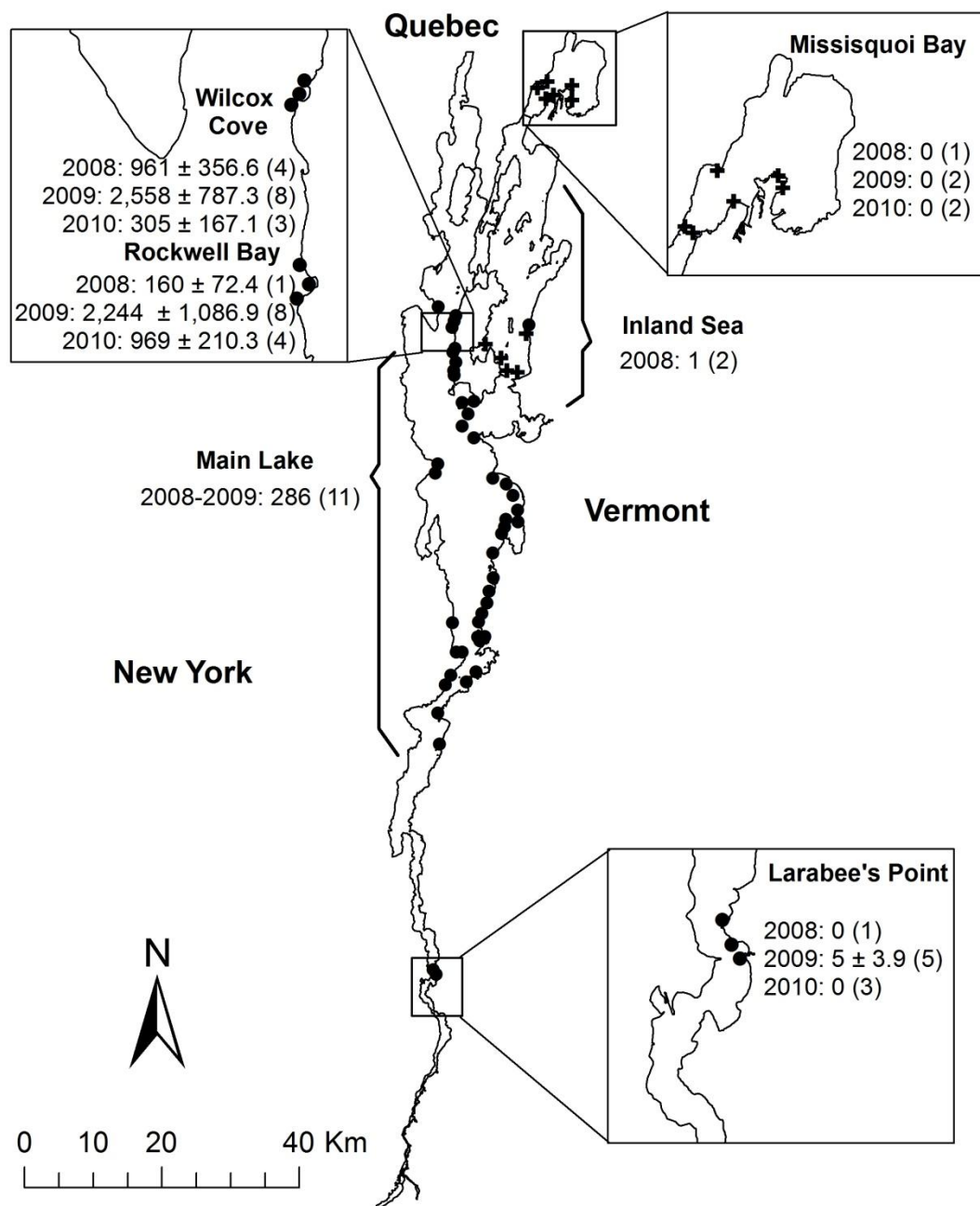


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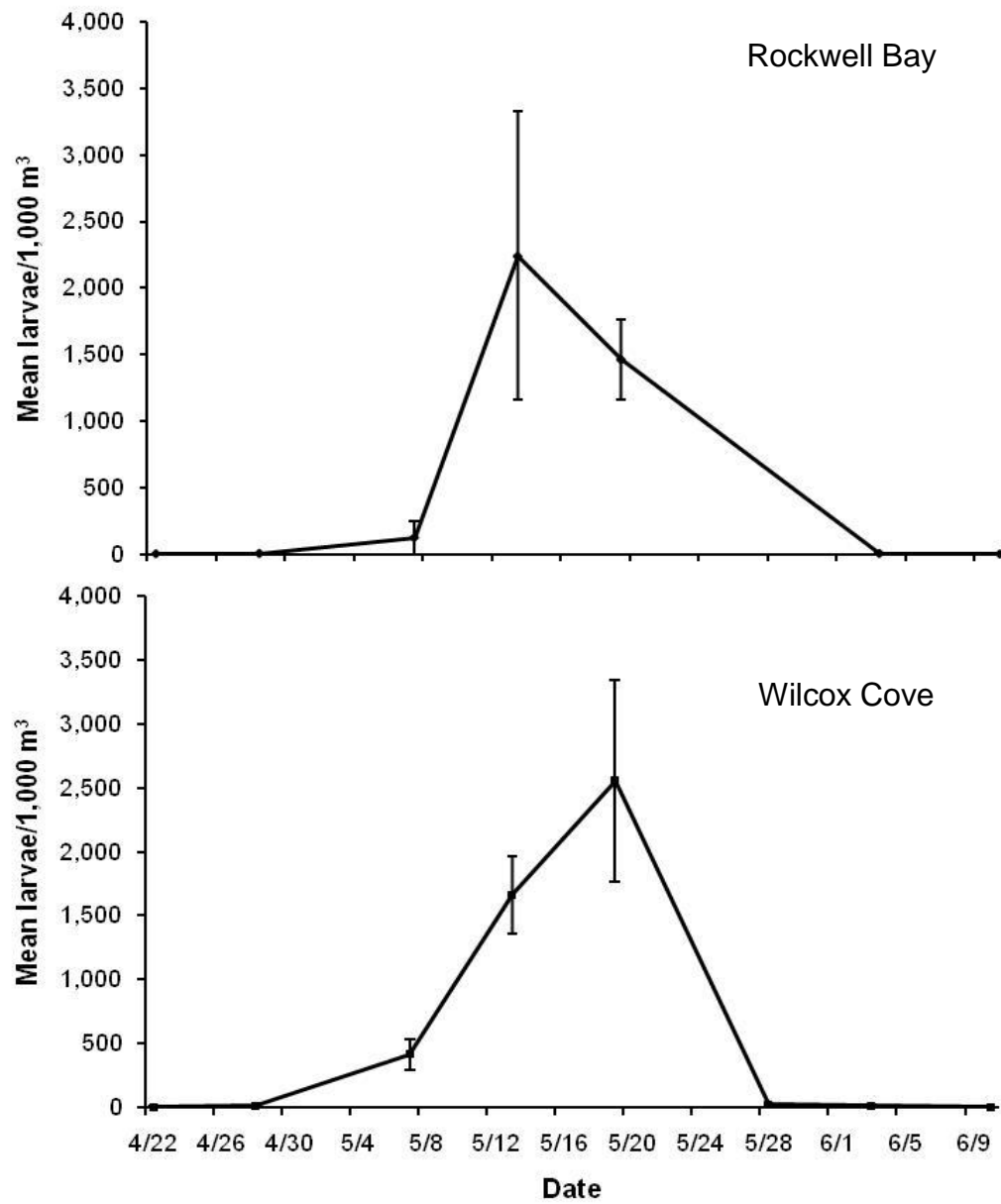


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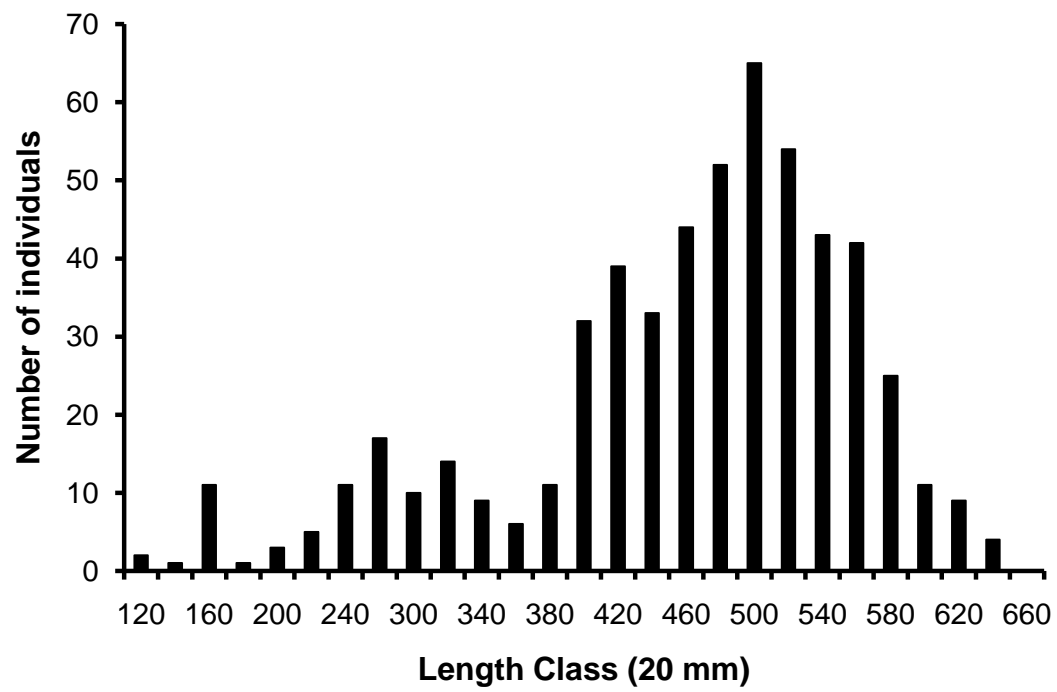


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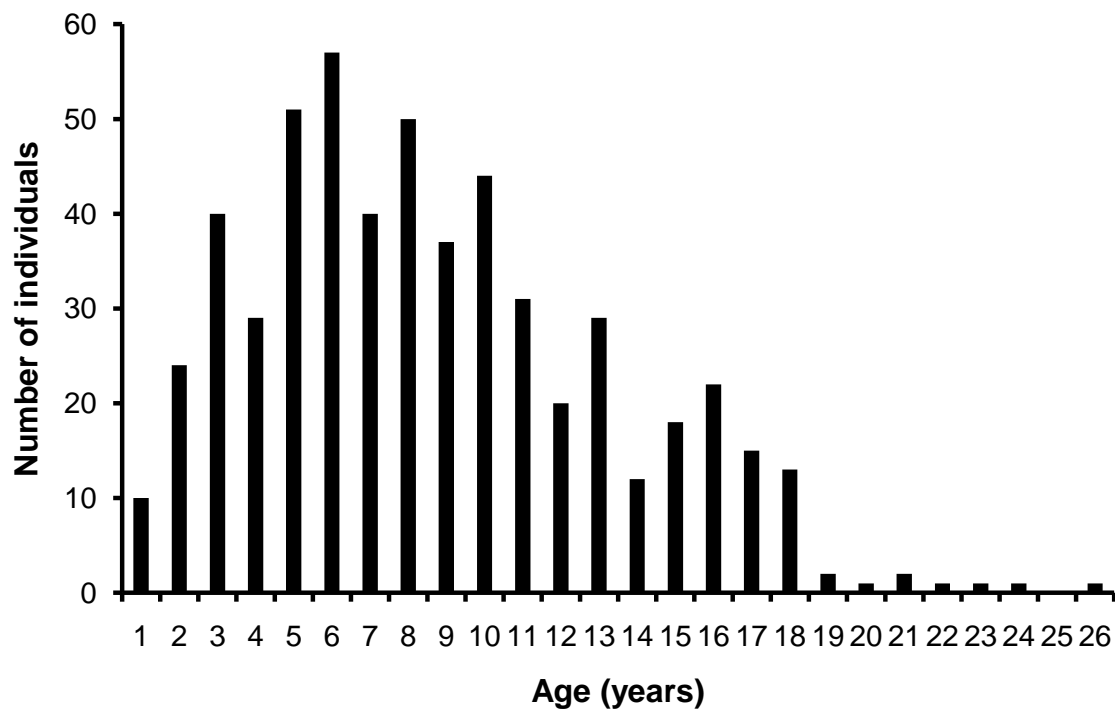


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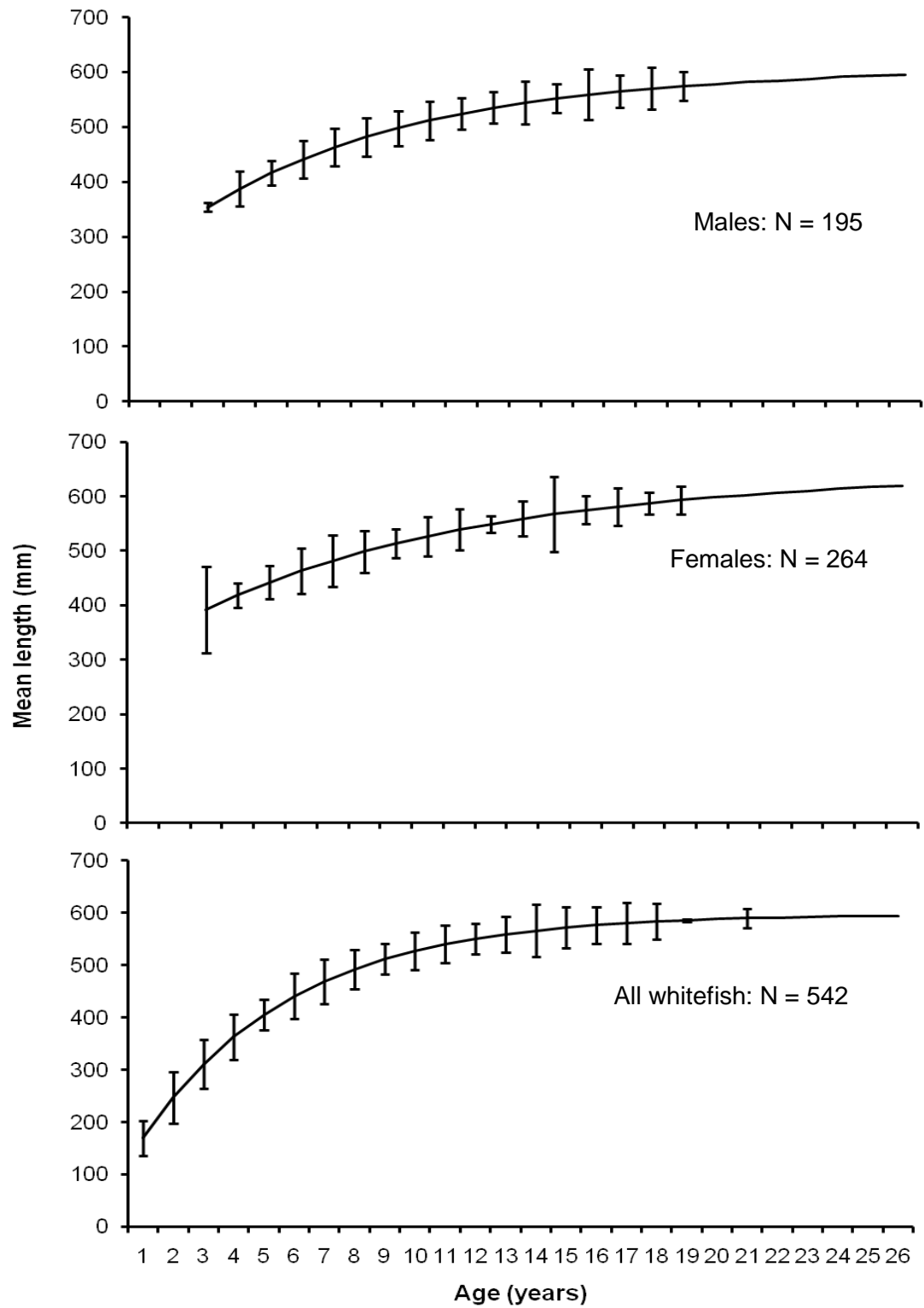


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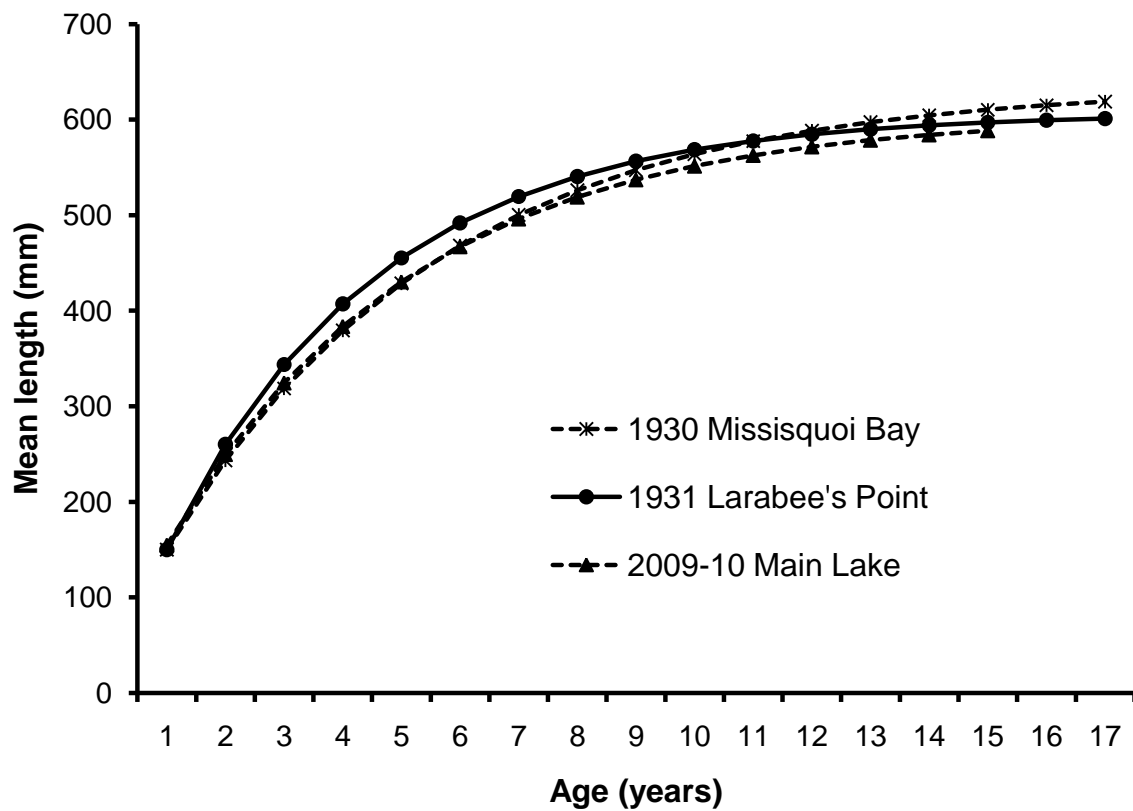


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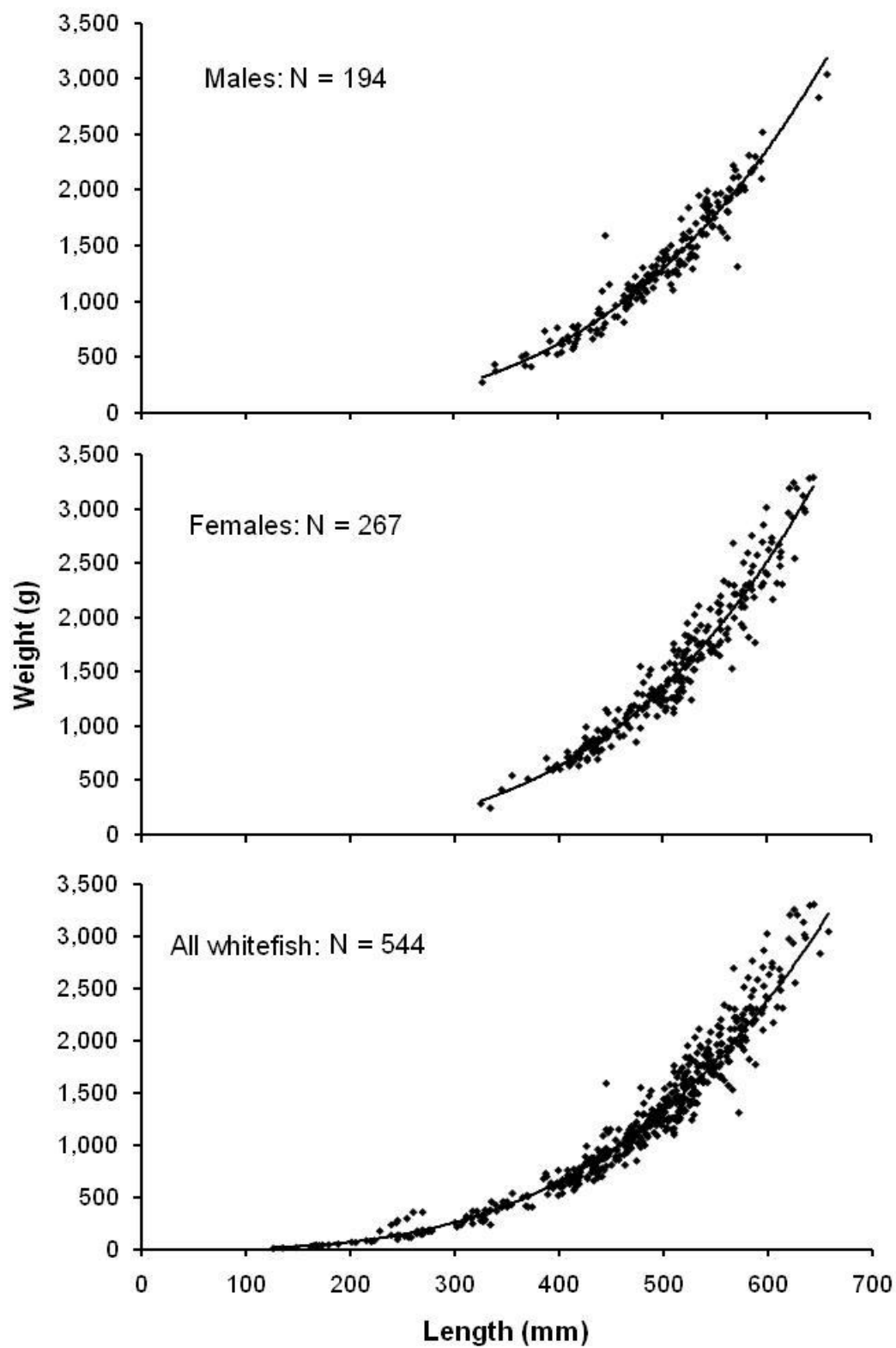


Figure 2.8

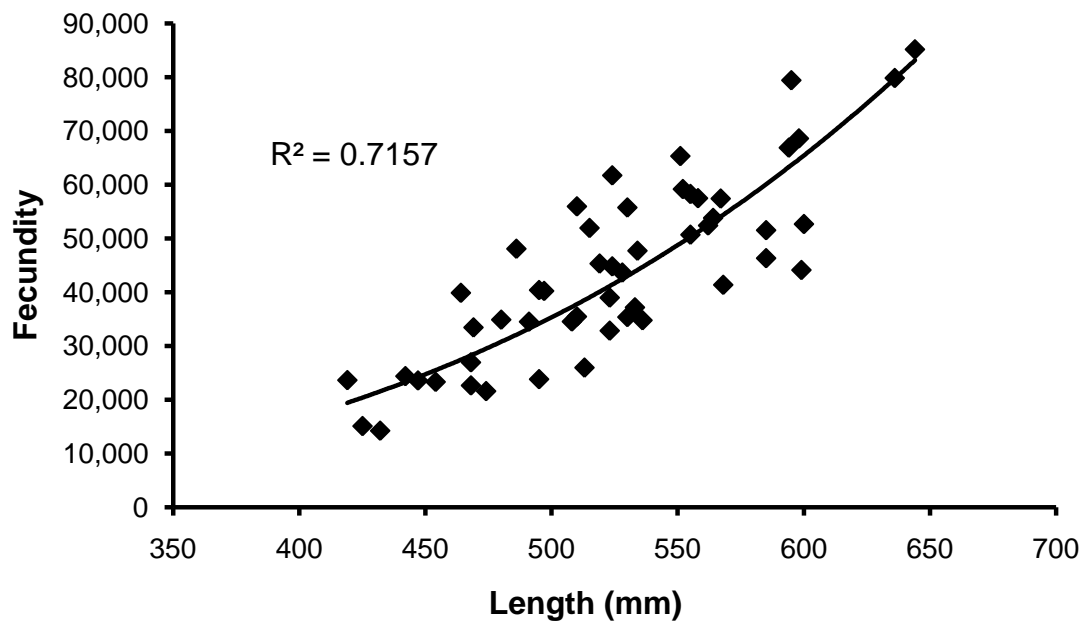


Figure 2.9

Chapter 3:

Lake Whitefish Diet, Condition, and Energy Density in Lake Champlain and the Lower Four Great Lakes Following Dreissenid Invasions

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Abstract

Lake whitefish (*Coregonus clupeaformis*) support one of the most valuable freshwater fisheries North America. In recent years, decreases have occurred in growth and condition of whitefish in the Great Lakes. Those decreases have been attributed to introduction of dreissenid mussels in the Great Lakes, and the consequent disappearance of *Diporeia*, a once-abundant native high energy prey source. Lake Champlain has also experienced the introduction and proliferation of zebra mussels (*Dreissena polymorpha*), but in contrast to the Great Lakes, *Diporeia* were not historically abundant. Our goal was to determine whether Lake Champlain whitefish have exhibited similar responses in diet, condition, and energy density, following the dreissenid mussel invasions, to whitefish in lakes Michigan, Huron, Erie, and Ontario. Whitefish were collected using gillnets and bottom trawls. Diet was quantified seasonally. Condition was estimated using Fulton's K and by determining energy density. Lake Champlain whitefish, unlike whitefish from the Great Lakes, did not show a dietary shift towards zebra mussels, but instead are feeding primarily on fish eggs in spring, *Mysis* in summer, and gastropods and sphaeriids in fall and winter. As a result, Lake Champlain whitefish condition and energy density were high compared to Great Lakes whitefish affected by dreissenids. Energy density of whitefish in Lake Champlain was similar to Lake Erie whitefish, a population that did not experience declines in growth and condition as the result of the introduction of dreissenids. In contrast to the Great Lakes, whitefish diet and condition in Lake Champlain do not appear to have been directly affected by the zebra mussel invasion.

Introduction

Large ecological changes caused by the introductions of exotic species have had negative affects on lake whitefish (*Coregonus clupeaformis*, hereafter, whitefish) in the Great Lakes. Whitefish are one of the most economically valuable freshwater species in North America, with the Great Lakes generating the majority of the commercial harvest. In 2008, 4.33-million kilograms of whitefish, valued at US\$8.1 million dollars, were harvested from the US waters of the Great Lakes (NMFS, 2008). Whitefish were also of historic importance to the Lake Champlain commercial fishery, with overall harvest and license sales peaking from 1895 to 1912, and an average annual whitefish yield of 18,537 kg/year (Halnon, 1963). The commercial fishery closed in 1913, and since then exploitation of whitefish in Lake Champlain has been limited to harvest by recreational anglers, which has historically been low (Anderson, 1978).

Declines of whitefish populations within the Great Lakes have been attributed to the introductions of exotic species such as rainbow smelt (*Osmerus mordax*), alewife (*Alosa pseudoharengus*), sea lamprey (*Petromyzon marinus*), and dreissenid mussels (*Dreissena polymorpha*, *D. bugensis*) (Ebener, 1997; Nalepa et al., 2005). Lake Champlain has also experienced introductions of alewife and zebra mussels, and sea lamprey wounding on lake trout (*Salvelinus namaycush*) and lake whitefish is high (Marsden and Hauser, 2009; Marsden et al., 2010). However, the affects of these species on whitefish are difficult to interpret because of the lack of historical information on whitefish in Lake Champlain.

Dreissenid mussels were introduced into the Great Lakes in the late 1980s and were established throughout the lakes by the early 1990s. The expansion of dreissenid

mussels was associated with major declines in native benthic invertebrate communities (Dermott et al., 1993; Dermott and Kerec, 1997; Dermott, 2001; McNickle et al., 2006; Bunnell et al., 2009). Dreissenids have high filtration rates and have been hypothesized to limit food availability for other benthic organisms (Horgan and Mills, 1997). For example, dreissenid mussels are thought to have caused the large declines of the once abundant native amphipod, *Diporeia*, in the Great Lakes (Nalepa et al., 1998; Dermott, 2001; Nalepa et al., 2005; Bunnell et al., 2009). Lake Champlain's native benthic community differed from the Great Lakes in that *Diporeia* were not historically abundant (Myer and Gruendling, 1979; Fiske and Levey, 1996). Instead, Lake Champlain's deepwater benthic community consisted mostly of gastropods, sphaeriidae, insect larvae, and *Mysis* (Myer and Gruendling, 1979; Fiske and Levey, 1996). Zebra mussels were introduced to Lake Champlain in 1993 and, because of their negative affects on the Great Lakes benthic communities, these mussels were thought to have the potential to negatively affect the benthos of Lake Champlain. However, Beekey et al. (2004) documented that the expansion of zebra mussels on soft sediments led to increased abundance and richness of benthic invertebrates in two bays of Lake Champlain.

In the lower four Great Lakes, declines in whitefish growth, condition, and energy density have been attributed to benthic community shifts, and loss of *Diporeia*, caused by dreissenid mussel introductions (Pothoven et al., 2001; Mohr and Nalepa, 2005; Madenjian et al., 2006; Pothoven et al., 2006; Lumb et al., 2007). These changes have been evaluated by estimating energy density, a surrogate for estimating growth potential, which is controlled by two factors: (1) energy content of a fish's diet and (2) feeding rate (Madenjian et al., 2000). Feeding rates tend to remain constant; therefore, the major

concern for growth potential is the energy content of the diet. Whitefish diets from the Great Lakes have been extensively studied following the proliferation of dreissenids, and have transitioned from high numbers of the energetically valuable amphipod, *Diporeia*, to large quantities of the low energy content dreissenid mussels (Pothoven et al., 2001; Mohr and Nalepa, 2005; Pothoven et al., 2006; Lumb et al., 2007). Energy density estimates of primary prey items, *Diporeia* and *Mysis*, are 3,625 J/g and 3,924 J/g, relative to 1,703 J/g for dreissenid mussels (Madenjian et al., 2006). Pothoven and Madenjian (2008) suggested that to achieve pre-invasion growth rates with the post-invasion diet composition, total consumption would have to increase by 78-122%, on average, over observed post-invasion consumption in Lake Huron because of the lower energetic intake from preying upon dreissenids. In contrast to the Great Lakes, the effects of the zebra mussel invasion on whitefish in Lake Champlain are unknown.

Our goal was to determine whether Lake Champlain whitefish have exhibited similar responses in diet, condition, and energy density, following the dreissenid mussel invasions, to whitefish in lakes Michigan, Huron, Erie, and Ontario (hereafter, Great Lakes). Our objectives were to (1) quantify seasonal diet and determine whether the invasion of zebra mussels caused a similar shift in whitefish diet in Lake Champlain as was found in the lower Great Lakes, (2) quantify condition, and (3) estimate energy density of whitefish in Lake Champlain for comparison with the Great Lakes. Lake Champlain diet was quantified as percent composition and frequency of occurrence of prey items and then compared with diet information from the Great Lakes. Condition was estimated for a post-dreissenid time period in Lake Champlain using Fulton's K and was compared with condition values (K) reported for the Great Lakes pre- and post-dreissenid

invasion. Lastly, energy density was estimated for individual whitefish from Lake Champlain and compared to estimates from studies conducted in the Great Lakes after the introduction of dreissenid mussels.

Methods

Study Area.— Lake Champlain is a long (~200 km), narrow (~12 km at its widest point), and deep (19.5 m average, 122 m max depth) lake with a surface area of 1,130 km². The lake is bordered by Vermont (east shoreline), New York (west shoreline), and the Province of Quebec (north). Lake Champlain is comprised of four basins, separated by geographic and man-made barriers, with varying watershed land uses (agriculture to forested), and trophic status (eutrophic to oligotrophic). Our study focused on the oligotrophic main lake basin near Proctor Shoal and Shelburne Bay (Figure 3.1). This area has a maximum depth of 43 m, and contains a cold-water fish community dominated by lake trout, lake whitefish, rainbow smelt, and, since the mid-2000s, alewife. Zebra mussels were first noticed in Lake Champlain in 1993 and have since expanded throughout the main lake, covering both hard and soft substrates (Beekey et al., 2004; Marsden and Hauser, 2009).

Fish collections

Whitefish sampling was conducted during the fall of 2006-2008 and year-round from 2009-2010 in the main basin of Lake Champlain (Figure 3.1). Fish were captured using a 7.6-m semi-balloon otter trawl (6.4-mm stretched-mesh cod-end liner) with a chain footrope, primarily targeting juveniles, and using short-term (3-4 hr) bottom-set gill nets to collect adults. Gill nets were 1.8 m deep and 70.6 to 152.4 m long, and included panels of 7.6, 8.9, 10.2, 11.4, 12.7, 14, and 15.2 cm stretch mesh. Whitefish were

weighed (nearest g) and measured (total length \pm 1 mm), otoliths were extracted and stored in labeled envelopes for age estimation in the laboratory, and stomachs (esophagus to the posterior end of the intestine) were removed and frozen individually for dissection in the laboratory.

Stomach dissection.— In the laboratory, stomachs were dissected and weighed as total wet weight (g) and all contents were removed, weighed (g, wet weight), identified taxonomically to family level, and counted. Stomach samples were separated into four seasonal categories: spring (April, May, and June), summer (July and August), fall (September and October), and winter (November through March). Only stomachs containing prey were used for analysis.

Data analysis

Diet.— Lake Champlain whitefish diet was quantified in two ways, (1) frequency of occurrence, describing presence or absence of prey items in each stomach, and (2) percent composition (by number), describing the number of items of a given prey type expressed as a percentage of the total number of items counted (Bowen, 1996).

We compared the diet of whitefish in Lake Champlain with the diets of whitefish from the Great Lakes following the invasions of dreissenids. Pre-invasion whitefish diets were not compared for Lake Champlain and the Great Lakes because Lake Champlain data are lacking. Post-invasion diet data from lakes Michigan and Huron were derived from 1,309 whitefish collected from 1998 to 2004 (Pothoven and Madenjian, 2008). Diet data for lakes Erie and Ontario were derived from seasonal sampling in 2003, reported by Lumb et al. (2007). We compared the proportion of diets that consisted of dreissenid

mussels to determine whether whitefish transitioned to preying upon the introduced mussels.

Condition.— Whitefish condition was estimated for Lake Champlain and the Great Lakes using Fulton's K condition factor (Anderson and Neumann, 1996),

$$K = \frac{W}{L^3} * 100,000$$

where W is observed weight and L^3 is the weight predicted by isometric growth when using metric units (mm and g). Fulton's K is strongly correlated with physiological estimates of body condition and has been found to have no biologically significant length-related bias for whitefish (Rennie and Verdon, 2008). Condition estimates were separated into pre- (1993 and earlier) and post-dreissenid (after 1993) invasion time periods for each lake with the exception of Lake Champlain, which was included only in the post-dreissenid analysis because of the paucity of pre-dreissenid weight-length data. Mean condition for Lake Champlain whitefish from 2009 and 2010 was estimated using age-4+ whitefish collected year-round, northern Lake Michigan (management units WFM-01, WFM-02, and WFM-03); Lake Huron estimates were calculated using unpublished data provided by Mark Ebener (Chippewa Ottawa Resource Authority); Lake Erie estimates were derived by averaging the annual condition means for male and female (age-4 and older) whitefish reported by Cook et al. (2005); Lake Ontario estimates were provided for females collected annually in the fall by Jim Hoyle (Ontario Ministry of Natural Resources, unpublished data).

We compared the mean condition value (K) for lakes Michigan (northern), Huron, and Erie before and after 1993 using a student's t-test to determine whether condition within lakes differed significantly ($P < 0.05$) before and after the dreissenid invasion. We

then used analysis of variance (ANOVA) to determine whether condition differed significantly between lakes before and after the invasion of dreissenids. Lake Ontario was excluded from these analyses because the weight-length data were limited to only females collected in the fall.

Energy density.— A sample of 52 whitefish collected in Lake Champlain from March to May 2010, ranging in size from 188-566 mm (TL), were analyzed for energy density. Whole individual whitefish with stomach and intestine removed (but other viscera intact) were processed in a Hobart 4822 meat grinder and homogenized in a mixing bowl. Small individual whitefish (< 250 mm TL) were processed and homogenized in a kitchen blender. A 25-50 g subsample from each homogenate was dried at 65-70 °C to a stable weight (approximately three days) to determine percent wet weight. Dried homogenate was then ground up using a Magic Bullet® blender to a fine powder and pressed into 3-4 pellets (approximately 1 g each) per fish. Pellets were ignited in a Parr Adiabatic bomb calorimeter to determine the number of joules per sample. The values for the 3-4 subsamples per fish were averaged and within-sample variability was estimated. Individuals that had high within-sample variability, which was thought to be caused by incomplete burning of the pellets, were excluded from analysis. The mean energy density (J/g) per fish was reported on a wet-weight basis for comparison with the Great Lakes.

Energy density estimates for whitefish from lakes Michigan, Huron, Erie, and Ontario were acquired from authors of previous studies (Pothoven et al., 2006; Lumb et al., 2007). Lake Michigan fish were collected from April to November from 2002-2003 and were processed as five-fish composites based on 25.4 mm size intervals (Pothoven et al., 2006). Lake Huron fish were collected from May to September from 2002-2004 and

were processed individually (Pothoven et al., 2006). Lake Erie and Lake Ontario fish were collected throughout the year during 2003 and were processed individually. To increase the sample size of fish with energy density estimates in lakes Erie and Ontario, the relationship between water content (WC, % mass) and energy density (ED, J/g wet weight) was used for individuals with known water content (Lumb et al., 2007). Methods for homogenization and energy density processing of whitefish from the Great Lakes were consistent with processing described for Lake Champlain fish (Pothoven et al., 2006; Lumb et al., 2007).

We plotted energy density against fish weight to investigate the effects of fish size on energy density from lakes Champlain, Huron, Erie, and Ontario. For Lake Michigan we plotted energy density against the mean weight of the five fish composites. Analysis of covariance (ANCOVA) with fish weight as the covariate was used to determine whether energy density of whitefish from Lake Champlain differed from whitefish in the lower Great Lakes.

Results

Diet— Whitefish diets differed among seasons in Lake Champlain during 2006 to 2010, but dominant prey items were consistent for each season between the two years (2009 and 2010) that were sampled for all seasons. In spring, whitefish fed primarily on large numbers of fish eggs and then transitioned to mysids in the summer and gastropods in the fall and winter (Table 3.1). Zebra mussels made up less than one percent of the diet; they appeared in less than ten percent of the stomachs analyzed (Table 3.1). The diet composition was diverse in all seasons, with multiple prey items making up large

portions of the diet. For example, in the summer, mysids, gastropods, and sphaeriidae were 61.2, 18.5, and 17.6 percent of the diet (Table 3.1). Gastropods did not always represent the highest number of prey items eaten in each season, but were the highest proportion of stomach contents in each season (Table 3.1). The percent of fish that had prey items in the stomach was consistent for all seasons except the fall, which had a greater percent of fish with empty stomachs (Table 3.1).

In contrast to Lake Champlain, diets of whitefish of lakes Ontario, Michigan, and Huron contained greater than 30% dreissenid mussels (Figure 3.2). Among the lakes, dreissenid mussels made up the greatest proportion (75%) of the diet in southern Lake Huron (Lumb et al., 2007; Figure 3.2).

Condition— Great Lakes whitefish body condition began declining in the late 1980s with more abrupt decreases in lakes Michigan, Huron, and Ontario following the expansion of dreissenids in the early 1990s, whereas Lake Erie whitefish condition did not change significantly (Figure 3.3, Table 3.2). Whitefish from lakes Erie and Champlain had similar, good condition estimates, whereas whitefish from lakes Michigan and Huron had similar, poor condition estimates since the arrival of dreissenids, based on Fulton's K (Table 3.2).

Energy density— We estimated energy density from 49 whitefish from Lake Champlain and compared those estimates with 240 whitefish from Lake Huron, 43 composite samples from Lake Michigan, 59 whitefish from Lake Erie, and 41 whitefish from Lake Ontario. Separate regressions relating energy density to weight for small (< 800 g) and large (≥ 800 g) whitefish were used because energy density increased with body weight up to approximately 800 g and then stayed constant with increases in weight (Table 3.3,

Figure 3.4). Energy density for small whitefish was highest overall in Lake Champlain and was significantly greater than lakes Huron ($F = 114.17$; $df = 1, 229$; $P < 0.01$), Michigan ($F = 25.91$; $df = 1, 50$; $P < 0.01$; Table 3.3), and Ontario ($F = 10.80$; $df = 1, 35$; $P < 0.01$), but similar to Lake Erie ($F = 0.46$; $df = 1, 40$; $P \leq 0.50$; Table 3). Energy density for large whitefish from Lake Champlain did not differ significantly from lakes Erie ($F = 1.27$; $df = 1, 62$; $P \leq 0.26$) or Michigan ($F = 2.18$; $df = 1, 37$; $P \leq 0.14$), but was significantly greater than lakes Huron ($F = 5.51$; $df = 1, 56$; $P \leq 0.02$) and Ontario ($F = 14.53$; $df = 1, 49$; $P < 0.01$).

Discussion

Whitefish in Lake Champlain have not transitioned to feeding on zebra mussels since the mussels were introduced to the lake in 1993. The high condition values for whitefish indicate that they have been attaining sufficient energy sources from their diet, which consisted primarily of fish eggs, mysids, gastropods, and sphaeriidae.

Physiological condition, estimated from energy density, was also high compared to whitefish from lakes Huron, Michigan, and Ontario and similar to whitefish in Lake Erie; in comparison with the other Great Lakes, Lake Erie whitefish have not been directly affected by dreissenid mussels.

Diets of whitefish from Lake Champlain changed seasonally, targeting large quantities of fish eggs in the spring, mysids in the summer, and gastropods and sphaeriids in the fall and winter. Most of these items, except fish eggs, are commonly reported in the diets of whitefish in other lakes (Owens and Dittman, 2003; Pothoven and Nalepa, 2006; Lumb et al., 2007; Pothoven and Madenjian, 2008). Fish eggs are often only seasonally

available in the cold-water benthic habitat occupied by whitefish, thus they are rarely reported in diet studies that tend to focus on the warm-weather seasons. However, fish eggs occurred in 66% of stomachs of whitefish captured during the winter in Lake Superior (Seider and Schram, in review).

Whitefish are commonly reported as non-selective feeders, showing variations in diet among different lakes, seasons, and depths that are consistent with prey availability (Hart, 1931; Pothoven, 2005; Pothoven and Nalepa, 2006; Pothoven and Madenjian, 2008). This non-selective feeding pattern is reflected in the increased consumption of dreissenid mussels by whitefish following increased abundance of the non-native mussels into many of the Great Lakes (Ihssen et al., 1981; Pothoven and Nalepa, 2006; Pothoven and Madenjian, 2008). Diet of whitefish in Lake Champlain, however, included minimal numbers of zebra mussels even though the exotic mussels are abundant in the lake's benthic community; this indicates that whitefish in Lake Champlain are actively avoiding consumption of zebra mussels. *Diporeia* were never abundant in Lake Champlain, however, so whitefish were never dependent upon the amphipod as a major food source (Fiske and Levey, 1996). Therefore, benthic community shifts caused by dreissenid mussel introductions, previously mentioned, have resulted in different foraging responses in Lake Champlain whitefish compared to what was seen in the Great Lakes.

When Lake Champlain whitefish diet data were averaged across all fish as percent composition, individual daily feeding strategies were masked. Some individual whitefish appeared to specialize on certain prey types, with individual fish consuming hundreds of individuals of a single prey type which was not necessarily the dominant prey item for the season. Similarly, Pothoven and Nalepa (2006) documented that individual whitefish

from Lake Huron had flexibility in diet with some individuals specializing on prey types that were not necessarily consistent with the overall diet composition for the population. Thus, although whitefish are generalist feeders, individual feeding strategies appear to be flexible and heterogeneous within populations (e.g., Warburton et al. 1998).

The amount of energy a fish acquires for the energetic costs of growth, reproduction, and maintenance is determined by its diet (Wootton, 1990). Pothoven and Nalepa (2006) found that energy in whitefish stomachs was lowest for fish that ate shelled prey; their findings were supported by the lower energy densities of whitefish preying upon large quantities of dreissenids in the lakes Michigan, Huron, and Ontario (Pothoven et al., 2006; Lumb et al., 2007). Body condition in fish is affected by the quality and quantity of diet items consumed; differences in energy densities among prey items affect the amount of energy input from the diet and thus affect the fishes ability to increase body mass (Ihssen et al., 1981). The diet of Lake Champlain whitefish consisted of prey items with high energy content such as fish eggs (6,243 J/g; Cummins and Wuycheck, 1971) and mysids and, as a result, these fish had high condition values. Whitefish populations in some locations in lakes Michigan, Huron, and Ontario were unable to find sufficient numbers of alternate prey after the dreissenid invasions and transitioned to foraging on dreissenid mussels, resulting in decreased energy intake and negative consequences on growth and condition (Hoyle, 2005; Mohr and Ebener, 2005). In contrast, Lake Erie whitefish condition did not decrease significantly after the dreissenid invasion; Cook et al. (2005) and Lumb et al. (2007) concluded that the invasion of dreissenid mussels in Lake Erie was not associated with reductions in growth

or condition because the fish were able to locate and prey upon a diverse assortment of other benthic prey remaining in the benthos.

Love (1980) noted that weight loss associated with decreases in energy reserves could be accounted for by an increase water content in fish, thus making it necessary to quantify condition using a more physiological method such as determining energy density (J/g). Physiological condition in Lake Champlain whitefish, determined by estimating energy density, was also high in comparison to the Great Lakes whitefish affected by dreissenids. Comparable to the length-weight condition estimate, energy density in whitefish from Lake Champlain was similar to data from Lake Erie for both small and large whitefish. Energy density of large whitefish from Lake Champlain was also similar to data from Lake Michigan, in contrast to the length-weight condition index comparison. This may be due to the proportion of mysids (30% by weight) in the diet of whitefish from Lake Michigan (Pothoven et al., 2006), which is similar to the proportion in Lake Champlain. Despite having similar *Diporeia* crashes in the Great Lakes, the two lakes that were most affected, lakes Michigan and Huron, had significantly different whitefish energy density estimates (Pothoven et al., 2006). These differences were attributed to differences in prey energy density, dissimilar diets, spatial variation, and the productivity of the lakes (Pothoven et al., 2006).

Many variables have the potential to influence the growth and condition of fish populations, many of which are density-dependent. Lumb et al. (2007) concluded that declines in growth and condition of whitefish from Lake Ontario were not related to density-dependent factors; however, in Lake Erie there were no changes in growth associated with annual changes in population densities; growth would be expected to

compensate for density dependent factors, with low growth in years of high population density. Although densities of whitefish in Lake Champlain are unknown, we presume that whitefish are not stressed from density-dependent factors based on a study on growth and condition (Chapter 2). Therefore, we conclude that Lake Champlain whitefish, similar to Lake Erie whitefish, have not had a negative response to the introduction of dreissenids because high-energy prey items are still available in the benthos and are being eaten by whitefish.

Despite the ecological changes to Lake Champlain following the introduction and expansion of zebra mussels in 1993, whitefish have not been directly affected. Whitefish have not transitioned to feeding on zebra mussels, and high length-weight condition values indicate that they have been attaining sufficient energy resources from their diet. Energy density of whitefish in Lake Champlain was similar to Lake Erie whitefish, a population within the Great Lakes that did not have declines in growth and condition associated with the introduction of dreissenid mussels. Therefore, we conclude that whitefish in Lake Champlain were not directly affected by the introduction of zebra mussels because growth and condition are at high levels indicating appropriate energy allocation from an assortment of prey items still available in the benthos.

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Table 3.1.— Seasonal diet composition (% by number) and frequency of occurrence for lake whitefish from Lake Champlain, 2006-2010. Seasons were defined as spring = April-June; summer = July-August; fall = September-October; winter = November-March.

Sample size (N) represents the number of stomachs that contained prey items.

Percent composition (by number)									
Season	Gastropods	Sphaeriidae	Zebra mussels	Insects	Fish eggs	Fish	Mysids	N	% empty
Spring	3.8	2.0	0.0	2.0	92.0	0.0	0.1	112	24.3
Summer	18.5	17.6	0.1	1.1	0.0	1.2	61.2	149	24.4
Fall	70.2	10.7	0.1	0.4	0.0	1.4	17.1	51	44.6
Winter	77.6	0.5	0.1	1.2	20.4	0.2	0.0	53	28.4
Frequency of occurrence									
Spring	50.9	75.0	0.9	30.4	42.0	4.5	7.1	112	24.3
Summer	66.4	60.4	2.0	11.4	0.0	24.2	57.0	149	24.4
Fall	64.7	29.4	5.9	13.7	0.0	31.4	19.6	51	44.6
Winter	81.1	9.4	9.4	11.3	17.0	9.4	1.9	53	28.4

Table 3.2.— Mean whitefish condition values using Fulton's K for Lake Champlain and the lower four Great Lakes before and after dreissenid invasions, with 1993 being the cut-off year between pre- and post-invasion periods. N represents the number of years used in the estimate of the overall mean K for both time periods. Insufficient weight-length data were available from Lake Champlain for the pre-dreissenid period. Different letters represent significant differences ($P < 0.05$) in condition between lakes within time periods. P-value indicates significant differences within lakes between time periods. Lake Ontario was excluded when comparing means between lakes because a different subset of fish (females only) was used.

Lake	Mean Fulton's K				P-Value
	Pre	N	Post	N	
Champlain	-	-	1.05 ^A	2	-
Erie	1.09 ^A	7	1.04 ^A	8	0.07
Michigan	1.01 ^B	9	0.87 ^B	15	< 0.01
Huron	0.96 ^C	9	0.88 ^B	15	< 0.01
Ontario	0.92	4	0.81	16	< 0.01

Table 3.3.— Linear regression coefficients for energy density (J/g wet weight) as a function of whitefish weight (g) in lakes Champlain, Erie, Ontario, Huron, and Michigan. Energy density estimates for lakes Michigan and Huron were derived from Pothoven and Madenjian (2008) and for lakes Erie and Ontario from the raw data summarized in Lumb et al. (2007).

Lake	< 800 g					≥ 800 g				
	α	β	r^2	P	Mean ED	α	β	r^2	P	Mean ED
Champlain	6,611	2.62	0.47	<0.01	7,799	8,722	-0.37	0.03	0.53	8,278
Erie	6,345	1.52	0.23	0.112	6,787	7,672	1.32	0.32	<0.01	9,483
Michigan	5,094	2.96	0.87	<0.01	5,851	7,258	0.27	0.04	0.34	7,591
Ontario	4,998	0.81	0.07	0.56	5,438	4,944	1.56	0.24	<0.01	7,256
Huron	4,556	1.64	0.32	<0.01	4,871	6,130	-0.22	0.0004	0.71	5,855

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Figure 3.1.— Map of Lake Champlain showing the study sites of Proctor Shoal (*) and Shelburne Bay.

Figure 3.2.— Proportion of whitefish diets comprised of dreissenid mussels following their invasion in lake Michigan, Huron, Erie, Ontario, and Champlain. Diet data were derived from Pothoven and Madenjian (2008) for lakes Michigan and Huron and Lumb et al. (2007) for lakes Erie and Ontario.

Figure 3.3 .— Trends in whitefish body condition (Fulton's K) for northern Lake Michigan, Lake Erie, Lake Ontario, Lake Huron, and Lake Champlain, 1986-2010. Dashed vertical line in 1993 indicated the year in which all lakes were impacted by dreissenid invasions. Lake Michigan and Lake Huron condition estimates were acquired from Mark Ebener (CORA), Lake Erie data were derived from Cook et al. (2005), and Lake Ontario data were supplied by Jim Hoyle (OMNR). Lake Ontario data are shown to depict trend in condition over time, but because estimates represent only females in the fall, values may be biased.

Figure 3.4 .— Energy density (J/g wet weight) separated by weight categories ($< 800\text{g}$ and $\geq 800\text{g}$ wet weight) of lake whitefish for lakes Champlain, Erie, Huron, Michigan, and Ontario following dreissenid invasion. Energy density estimates were derived from raw data summarized in Pothoven and Madenjian (2008) for lakes Michigan and Huron and Lumb et al. (2007) for lakes Erie and Ontario.

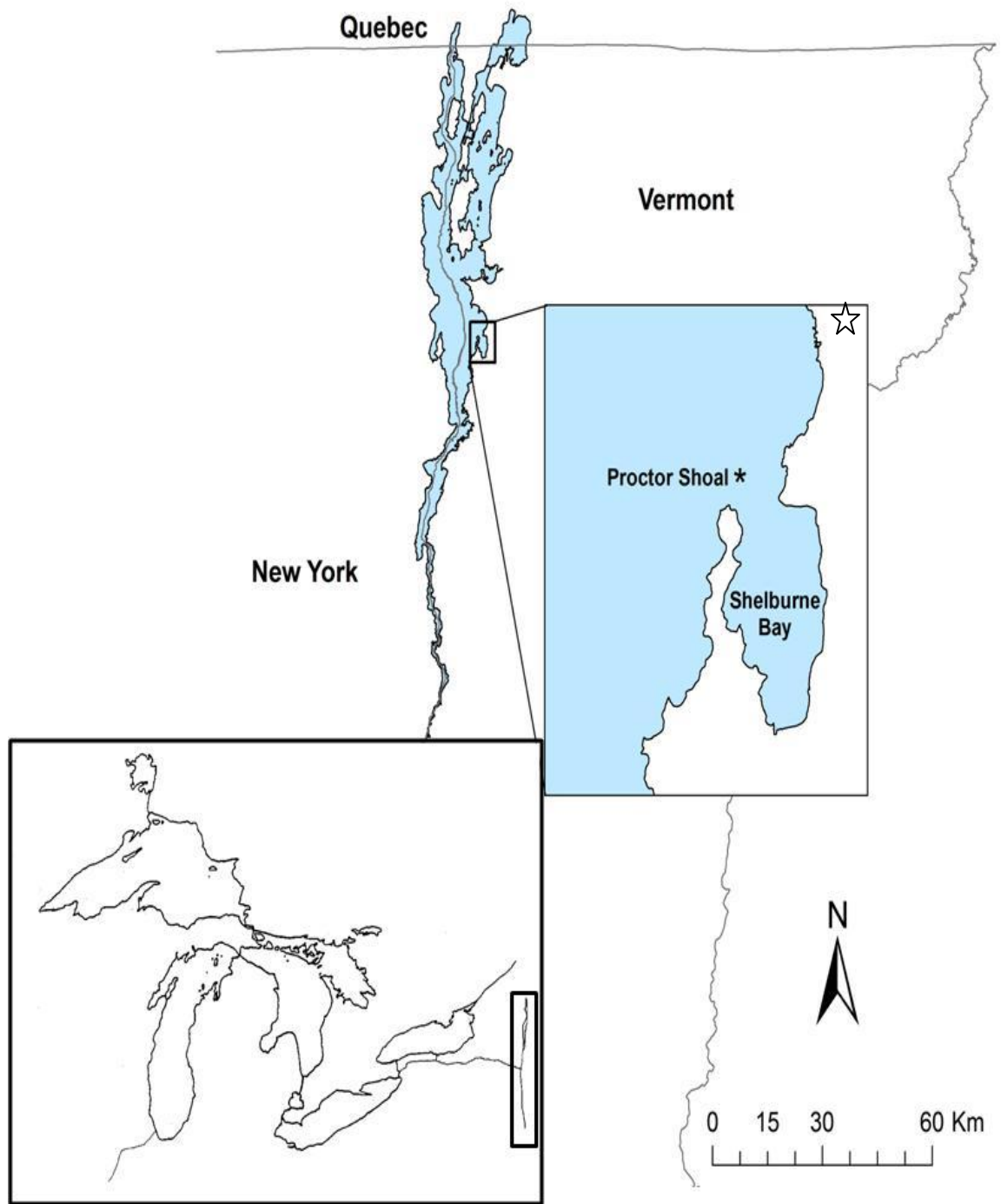


Figure 3.1

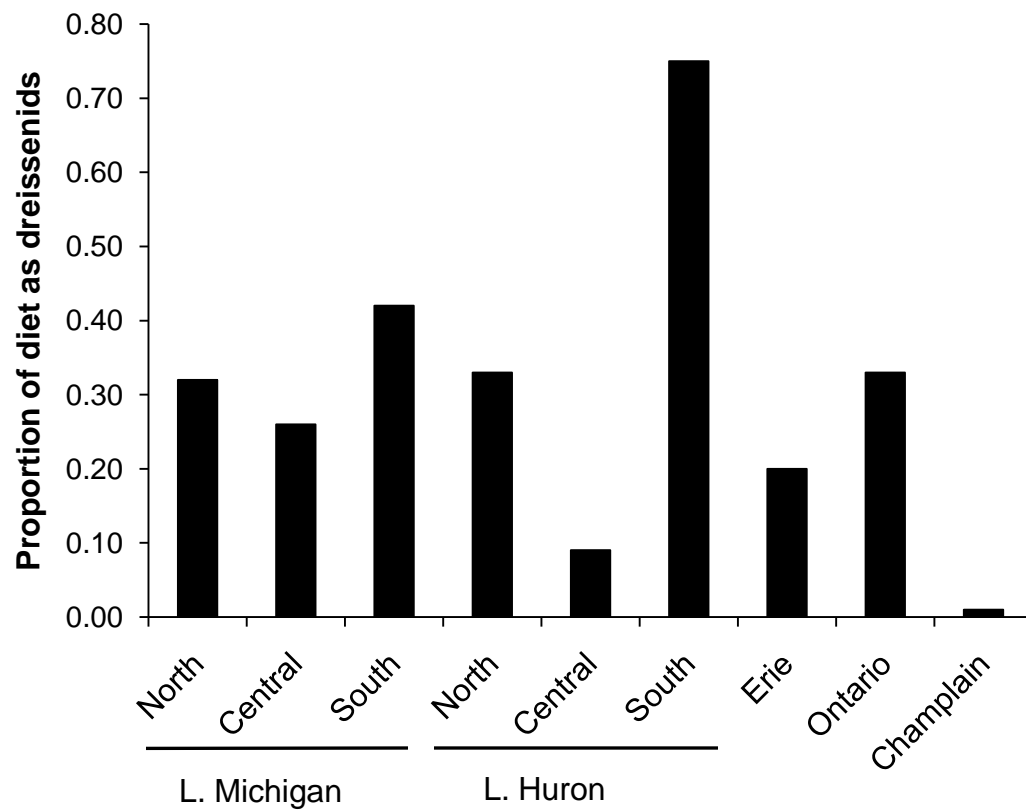


Figure 3.2

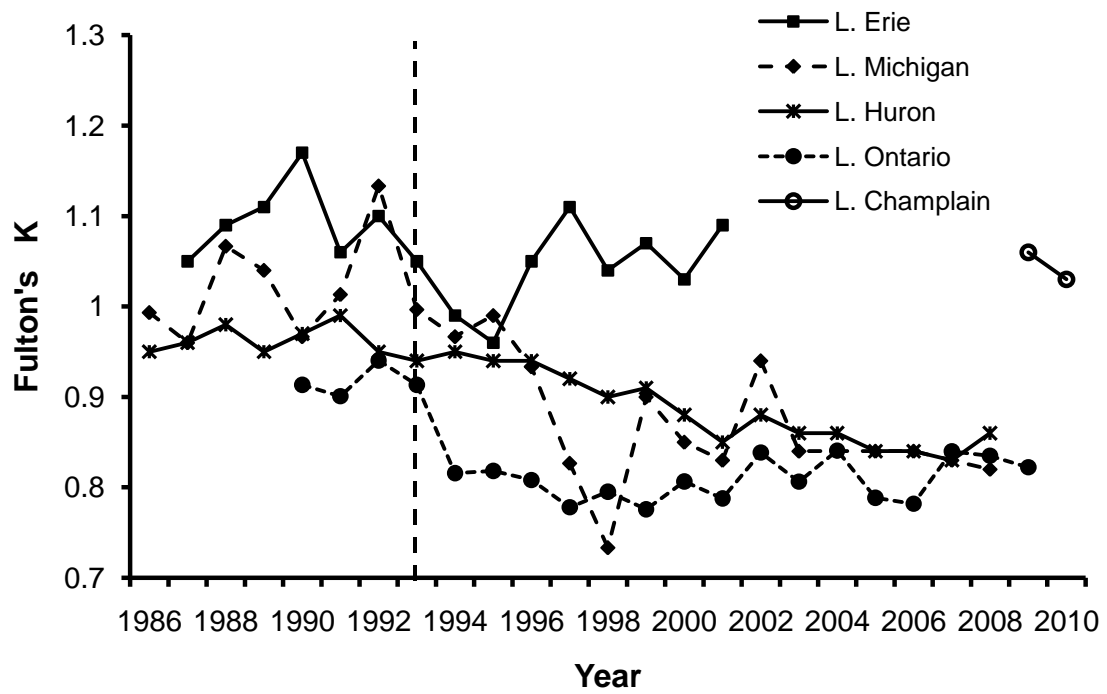


Figure 3.3

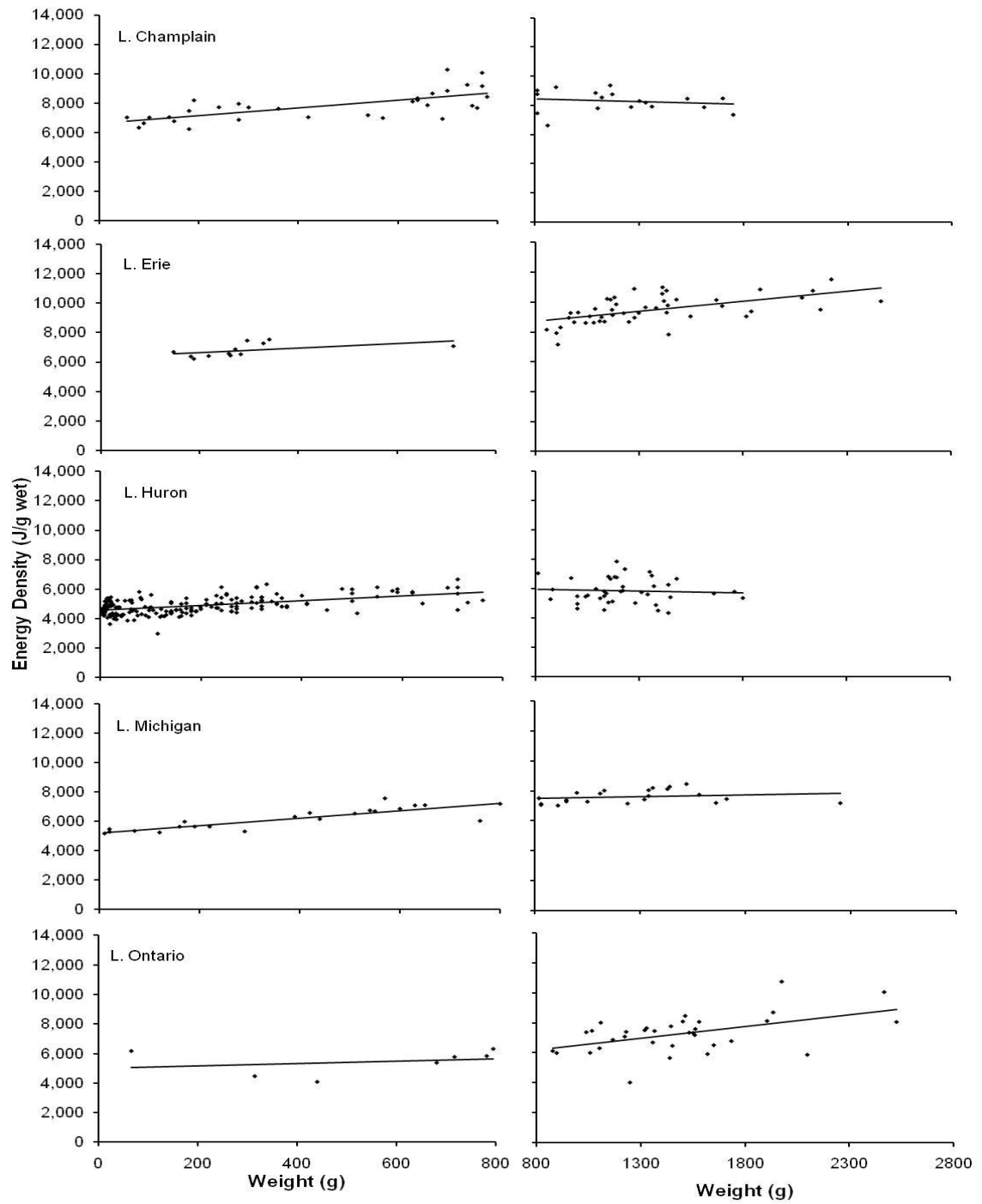


Figure 3.4

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